VARIABILITY IN STELLER SEA LION (*EUMETOPIAS JUBATUS*) PREY QUALITY IN SOUTHEASTERN ALASKA

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A

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GENERAL INTRODUCTION

Populations of piscivorous predators from multiple taxa have declined significantly in the North Pacific Ocean and Bering Sea since the 1970's. In particular, the western population of Steller sea lions has declined by over 80% and is listed as endangered (Burkanov et al. 2003; Sease et al. 2001; U.S. Federal Register 1997; Sease et al. 1993). The first chapter of this thesis reviews Steller sea lion population declines and the evidence for the nutritional stress hypothesis, which asserts that the declines are due to a lack of availability of quality prey. The second chapter addresses the two premises upon which the nutritional hypothesis is founded, namely: (1) prey quality of a single prey species is consistent among individuals and over time, and (2) forage fish are consistently superior quality prey items to groundfish. This study assesses these premises through systematic sampling of prey quality of several important Steller sea lion forage species measuring energy content and proximate composition.

CHAPTER 1

Literature review: Steller sea lion (*Eumetopias jubatus*) population decline[1]

Johanna J. Vollenweider

ABSTRACT

Since the late 1960's, significant declines in piscivorous pinniped and seabird populations have occurred in the Gulf of Alaska and Bering Sea. Of particular concern is the stock of Steller sea lions (*Eumetopias jubatus*) residing west of 144° West longitude that has declined by over 80% in the last 30+ years, resulting in their classification as an endangered species in 1997 under the U.S. Endangered Species Act (Burkanov et al. 2003; Sease et al. 2001; U.S. Federal Register 1997; Sease et al. 1993) (Figure 1). Because of the magnitude of their decline, Steller sea lions have been studied intensively, and may provide insight as to the other piscivorous predators with similar declining populations. From the collective research, a leading hypothesis was formed which asserts that nutritional stress induced from an altered prey base was the most probable cause of the declines during the 1970's and 1980's when declines were most severe (Trites & Donnelly 2003; Castellini 1993). At that time, shifts in the diet composition of sea lions reflected a change in the fish assemblages of the North Pacific Ocean, from a previous domination by forage fish to one by groundfish. Studies of free-ranging and captive sea

[1] Chapter 1 not submitted to a manuscript for publication.

lions indicate that deteriorations in sea lion health correlate with the consumption of groundfish which have been characterized as 'energy-poor' as opposed to 'energy-rich' forage fish. Consequently, the 'junk food hypothesis' was formed, attributing the decline in predator populations, particularly Steller sea lions, to a lack of availability of quality prey. The following chapter is a review of the evidence leading to the formulation of this hypothesis.

LITERATURE REVIEW

Since the late 1970's, piscivorous pinniped and seabird populations have declined significantly throughout the Gulf of Alaska and Bering Sea. Several species of murres and kittiwakes in the Pribilof Islands, the nesting area for the largest concentration of ledge-nesting seabirds in Alaska, have declined by as much as 50% between the mid-1970's and the late 1980's (Byrd 1989). Harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, once the site of one of the world's largest concentrations of the seals, have declined by as much as 85% between the late 1970's and late 1980's (Pitcher 1990). Similarly, Northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands have declined contrary to expectations of increased productivity after the cessation of commercial harvesting in 1968 (Trites & Larkin 1989). Over the same time period, the stock of Steller sea lions residing west of approximately 144° W longitude or Cape Suckling, Alaska have declined by more than 80% (Sease et al. 2001; Sease et al 1993), and have been on the U.S. Endangered Species list since 1997 (U.S. Federal Register 62:24345-24355).

Many hypotheses have been suggested as the cause of the population declines, including competition with fisheries, environmental change, nutrition, predation, disease, contaminants, entanglement, and shootings. Large numbers of dead animals have not been observed, suggesting predation or another cause chronic in nature which would result in a lowering of animals' reproductive success rather than having acute effects (Castellini 1993). Limited baseline data exists on the health of wild sea lions prior to the

population declines, making pre- and post- decline comparisons difficult. The existing data suggest, however, that Steller sea lion health deteriorated in a manner consistent with symptoms of nutritional stress based on observations such as the portion of the population declining most drastically as well as physiological attributes of individual animals (Pitcher et al. 1998; Calkins & Goodwin 1988).

On a population level, indications of reduced health include the overall decline in numbers with the greatest rate of decline having occurred in the juvenile portion of the population resulting in a shift in age structure towards older animals (York 1994). Elevated juvenile mortality is suggestive of either predation or a compromised nutritional state as young animals are more susceptible to dietary limitations due to their undeveloped diving aptitude, lack of foraging experience, and relatively higher energy demands (Winship et al. 2002; York 1994; Calkins & Goodwin 1988; Merrick et al. 1988). Symptoms of nutritional stress are also apparent in morphological and physiological attributes of individual animals. Sea lions, particularly juveniles, have smaller masses than they did in previous decades and have become shorter and thinner, indicating a reduced ability to grow and amass blubber reserves (Castellini & Calkins 1993; Calkins et al. 1998; Calkins & Goodwin 1988). Reproductive failures have also increased, especially in small and lactating females (Pitcher et al. 1998; Calkins & Goodwin 1988; Pitcher & Calkins 1981). Abortion is speculated to be an adaptive strategy for sea lions during times of sub-optimal nutrition (Pitcher et al. 1998). In addition, blood analyses implicate anemia which may be caused by dietary deficiencies

(Calkins & Goodwin 1988). Together, these lines of evidence indicate that sea lions in regions of population decline may have suffered nutritional stress as a result of a shortage of quality prey (Trites & Donnelly 2003; Castellini 1993).

In the late 1970's, coincident with the onset of the predator declines, the species composition of the North Pacific Ocean fish shifted from a previously diverse assemblage of forage fish to one in which a few species of groundfish predominated (Hare & Mantua 2000; Anderson & Piatt 1999; Francis et al. 1998; Mantua et al. 1997; Alverson 1992). Forage species that declined significantly during this reorganization included Pacific herring (*Clupea pallasii*) which decreased by 75% in the Northeast Pacific Ocean and eulachon (*Thaleichthys pacificus*) which decreased in CPUE from 13 kg/hr in trawl surveys to virtually no catch in the eastern Bering sea (Alverson 1992; Fritz et al. 1991). In addition, capelin (*Mallotus villosus*) virtually disappeared from the Gulf of Alaska while Pacific sandlance (*Ammodytes hexapterus*) abundance decreased as well (Piatt & Anderson 1996; Alverson 1992). Alverson described similar declines in shellfish including red king crab (*Paralithodes camtschaticus*) and pink shrimp (*Pandalus eous*) and fish species including Pacific ocean perch (*Sebastes alutus*) throughout its range and Atka mackerel (*Pleurogrammus monopterygius*) in the Gulf of Alaska (1992).

As forage fish and shellfish abundance declined, groundfish proliferated. Walleye pollock (*Theragra chalcogramma*) increased nearly three-fold to approximately eleven million metric tons in the mid-1980's (Fritz et al. 1991; Marasco & Aron 1991; Quinn & Collie 1990). Pacific cod also increased rapidly during the late 1970's and into the

1980's, as did many species of flatfish including Bering Sea yellowfin sole (*Limanda aspera*), flathead sole (*Hippoglossoides elassodon*), southern rock sole (*Lepidopsetta bilineata*), and Alaska plaice (*Pleuronectes quadrituberculatus*) (Alverson 1992). The reorganization of fish assemblages occurred through the Gulf of Alaska and Bering Sea, indicating that the mechanism of change was itself broad in range (Hare and Mantua 2000).

One factor influencing the change in the species composition of fish in the North Pacific Ocean was the 'Pacific Decadal Oscillation' (PDO), which causes abrupt climatic shifts or 'regime shifts' over broad areas on roughly multi-decadal periods (Hare & Mantua 2000; Mantua et al. 1997). The climatic changes affect the strength of regional weather systems such as the Aleutian Low, which alter atmospheric pressure, surface wind stress, and air-sea heat exchange. These factors in turn affect the temperature and depth of the mixed layer in which primary productivity occurs, causing sea surface temperatures to alternate between warm and cold phases (Francis et al. 1998; Gargett 1997). A dichotomy in climatic and thus oceanographic conditions occurs between the coastal Pacific Northwest and the central North Pacific Ocean. During warm phase conditions, sea surface temperatures in the central North Pacific Ocean are relatively cold while near-shore temperatures throughout the Gulf and southeastern Alaska are anomalously high. Associated with warm phases is enhanced biological production in Alaska and decreased production off the west coast of the contiguous United States. Conditions reverse during cool phases (Mantua et al. 1997). The cyclic nature of climatic

and oceanographic states creates conditions in which primary productivity and consequently upper trophic levels are selectively favored. Thus, the changes in climatic and oceanographic conditions may ultimately result in a reorganization of the entire community structure (Francis et al. 1998; Gargett 1997). Such a regime shift from cool to warm phase conditions occurred in the winter of 1976/1977, and is thought to have played a relatively large role in the depletion of forage fish and crustaceans and proliferation of groundfish (Hare & Mantua 2000; Mantua et al. 1997).

Another factor that may have influenced the changing fish assemblages was the intensification of commercial fisheries and whaling. Over the period of 1950 to 1990, explosive growth and development of fisheries in Alaska occurred, the Bering Sea and Gulf of Alaska pollock fishery becoming the world's largest single species fishery. Other significant emerging fisheries during the latter half of this century include driftnet salmon fisheries, as well as international and U.S. herring, groundfish, crab, and shrimp fisheries (Alverson 1992). Advances in commercial fisheries resulted in escalating catches in the Pacific Ocean rising from 2 million tons in the late 1940's to over 50 million tons in the early 1990's (Trites et al. 1997). Burgeoning fisheries may have caused species depletions, resulting in a change of ecosystem trophic dynamics (Alverson 1992). During the same time period, commercial whaling gained momentum with the development of at-sea processing. In the North Pacific whale harvests increased from approximately 2,000 whales annually in the early 1940's to peak harvests of nearly 25,000 in the late 1960's, continuing until the 1986 moratorium imposed by the International Whaling

Commission (International Whaling Commission 2003). The magnitude of top-level predator removal may have reduced competition for particular food resources, particularly zooplankton, opening a niche for the growing populations of pollock to occupy (Trites et al. 1999; Merrick 1997). In concert, climatic changes, commercial fishing, and whaling may have contributed to the changes in species assemblages in the North Pacific following the 1970's.

Foraging dynamics of many of the declining predator populations reflected the changing fish assemblages, including that of Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*), harbor seals (*Phoca vitulina*), black and red-legged kittiwakes (*Rissa sp.*), common murres (*Uria aalge*), marbled murrelets (*Brachyramphus marmoratus*), and horned and tufted puffins (*Fratercula sp.*) (Merrick et al. 1997; Merrick & Calkins 1996; Piatt & Anderson 1996; Sinclair et al. 1994; Calkins & Goodwin 1988; Perez & Bigg 1986; Pitcher 1981). Steller sea lion prey include over 60 species, though individual animals typically consume several taxa per feeding bout as inferred from scats (Trites et al. 2003; Sinclair & Zeppelin 2002; Merrick 1995; Pitcher 1981). The overall diversity of prey items suggests sea lions are opportunistic and can be considered samplers of the marine environment and thus are subject to variations in prey species recruitment and availability (Trites 1998; Sinclair et al. 1994). It can be expected that sea lion diet composition would reflect their changing prey base. During the cool phase of the 1950's, prior to the onset of the population declines, limited samples of Steller sea lion stomach contents suggested diets were dominated by cephalopods,

bivalves, smelt, sandlance, rockfish, and halibut with less than 5% of the total volume accounted for by walleye pollock (Mathisen et al. 1962; Thorsteinson & Lensink 1962; Wilke & Kenyon 1952). Following the 1976/1977 regime shift to warm phase conditions, walleye pollock or Atka mackerel become the predominant prey items for all ages of sea lions, across all seasons and locations, while other diet items such as Pacific herring, capelin, Pacific cod, and cephalopods were consumed in smaller quantities (Calkins 1998; Merrick & Calkins 1996; Calkins & Goodwin 1988; Pitcher 1981). The forage fish that persisted in the predator diets in relatively small amounts were often ephemeral resources that were restricted to temporally- and spatially-specific spawning events (Merrick & Calkins 1996).

The reduction in diet diversity following the regime shift is postulated to be an important factor in the sea lion decline (Merrick et al. 1997; Merrick & Calkins 1996; Piatt & Anderson 1996; Sinclair et al. 1994; Calkins & Goodwin 1988; Perez & Bigg 1986; Pitcher 1981). Diet diversity also correlated closely with region-specific Steller sea lion population trajectories (Trites et al. in press; Merrick 1995). Furthermore, no study of Steller sea lion diet has found a stable or increasing population maintained on a diet composed primarily of walleye pollock or Atka mackerel (Merrick et al. 1997). As such, diet diversity has been considered tantamount to diet quality, allowing for predators to obtain nutritional requirements despite deficiencies in some prey species. A diversity of prey also reduces the energetic costs of searching, capture, and handling. Thus, a reduction in the species diversity of Steller sea lion prey may be a factor causing

nutritional stress (Rosen & Trites 2000; Merrick et al. 1997; Merrick 1995; Castellini 1993).

Captive feeding studies have examined health effects of diet compositions characteristic of those consumed by free-ranging animals prior to and during the population declines. Sea lions fed solely pollock or mixed diets reminiscent of post-regime shift diets exhibited symptoms of malnutrition, including loss of body mass, decreased blubber stores, metabolic depression, and changes in body composition. In contrast, animals fed herring and diets of mixed forage fish species to simulate diets prior to sea lion declines appeared healthy, either maintaining or gaining mass (Donnelly et al. 2003; Rosen & Trites 2002; Calkins et al. 2000; Rosen & Trites 2000; Rosen & Trites 1999). Similar indications of nutritional deficiencies were observed in studies where diets of cephalopods were fed to other pinniped species as well as laboratory rats (Donnelly et al. 2003; Kirsch et al. 2000).

Feeding studies comparing ground-fish and forage-fish diet compositions have elucidated differences in their physiological effects on sea lions. Digestive efficiency, the gross ingested energy less excreted fecal energy or the percentage of prey energy that is retained, is significantly less for pollock than herring (Rosen & Trites 2000). In addition, pollock induce a higher heat increment of feeding than herring, causing increased heat production associated with meal ingestion from mechanical and biochemical breakdown of food and subsequent protein synthesis and somatic growth. Elevated heat increment of

feeding translates into greater energy requirements to digest a meal (Rosen & Trites 2000; Rosen & Trites 1997).

The next logical step in the investigation of nutritional stress is to assess the 'quality' of the biochemical composition of the alternate ground-fish and forage-fish diets. Prior to making inferences about the health ramifications for sea lions, however, prey 'quality' must first be defined. Simply stated, the definition of a 'quality' prey item is forage which meets a predator's nutritional requirements for maintenance, growth, activity and reproduction (Owen 1980). Nutritional requirements of Steller sea lions and other pinnipeds are poorly known, particularly with regard to specific nutrient needs. Aquaria husbandry consists of natural forage species with supplementation ranging from heavy to none (L. Mazzaro, Mystic Aquarium & Institute for Exploration, 55 Coogan Blvd. Mystic, CT 06355-1997 personal communication). Energy content, the universal currency of bioenergetics, is a typical method used to assess prey 'quality'. Sea lion energy requirements, measured directly in feeding studies and estimated indirectly through bioenergetic models increase with age and are greater for males. In addition, energetic requirements vary seasonally for mature, breeding animals. On average, pups require 37 MJ d^{-1}, while mature females and males require 88 MJ d^{-1} and 165 MJ d^{-1}, respectively (Winship et al. 2002; Kastelein et al. 1990). In comparison, humans require approximately 8 MJ d^{-1} based on a 2000 calorie diet.

Nutritional quality should also consider proximal composition, including lipid, protein, carbohydrate, water, and ash content, the dominant constituent components of all

organisms (Schmidt-Nielsen 1990). Proximal composition requirements are complementary to energy requirements for several reasons. Only lipid, protein, and carbohydrate provide energy, and thus proximal composition identifies the sources of energy, not all of which are equally useful (Watt & Merrill 1963; Brody 1945). Energy content is not transferred 100% efficiently to the consumer due to metabolic costs, with the energetic cost of catabolizing lipid the lowest (4-15%), intermediate for carbohydrates (4-30%) and highest for protein (30-70%) (Blaxter 1989). Further limiting the transfer of nutrients to the consumer is a predator-specific discrepancy in assimilation efficiency, the proportion of energy consumed that is not excreted. Steller sea lions have high assimilation efficiencies in general (>90%), however, prey with higher lipid and consequently higher energy content appear to be digested more efficiently than low-fat prey (Rosen & Trites 2000).

Though requirements for lipid, protein, water, and ash are poorly known for pinnipeds, daily dietary 'allowances' or best estimates have been made. Sea lion daily protein allowance is estimated at 0.043% of their body mass, while that of seals and walrus are 0.048% and 0.031%, respectively (Scott 1986). In comparison, a protein allowance for humans has been estimated to be 0.068%. Pregnancy and lactation incur additional requirements, with increases of 41% and 31% above the maintenance level for human females (Scott 1986). In general, carnivores require relatively high maintenance levels of protein, maintenance levels ranging from 18-34% of their ingested prey biomass, while juveniles and reproductive individuals require greater amounts (Robbins

1993). Fadely et al. (1994) suggested that pinnipeds may just be meeting their protein needs as they feed on diets ranging in protein content between 10-20% (Anthony 2000; Payne 1999; Van Pelt 1997).

Lipid requirements are more difficult to estimate, particularly for marine mammals which have lipid metabolism processes unique from terrestrial animals (Robbins 1993). It has been the general assumption that more lipid is better (Trites & Donnelly 2003; Rosen & Trites 2000; Castellini 1993). Lipid is the principal substrate from which energy is derived in the marine environment (Robbins 1993). Optimal foraging theory predicts that animals strive to forage in the most efficient manner possible, i.e. getting the highest profit with the least expenditure (Owen 1980). Foraging in the marine environment is expensive due to the large, three-dimensional search area and the patchy nature of prey aggregations, and thus energy is at a premium. In addition, fattier fish are better sources of essential fatty acids (Vanderhaeghe & Karst 2003). Similarly, fat soluble vitamins generally occur in proportion to the lipid content, and thus a fattier fish would have greater lipophilic vitamin content (Stansby 1976).

In addition to proximal composition, a variety of micronutrients are essential to animal nutrition, including vitamins, minerals, essential amino acids (EAA) and essential fatty acids (EFA). Those that are particularly important are the essential nutrients which can not be synthesized by the body and must therefore be obtained in the diet. Lack of any essential nutrient results in malnutrition and deficiency diseases (Robbins 1993;

Henderson & Tocher 1987). Micronutrients require multiple chemical analyses and will not be addressed further.

Preliminary direct measurements of the biochemical composition of forage fish and groundfish indicate diet quality has declined following the regime shift (Rosen & Trites 2000; Castellini 1993). Forage fish such as herring and eulachon have been characterized as relatively lipid-rich and thus energy-rich, while pollock and flatfish are typified as relatively lipid- and energy-poor (Iverson et al. 2002; Anthony et al. 2000; Payne et al. 1999; Robards et al. 1999; Paul et al. 1998; Van Pelt et al. 1997; Worthy & Miculka 1997; Perez 1994; Sidwell 1981; Stansby 1976). Accounting for the differences in energy content, digestive efficiency, and induced heat increment of feeding, herring and pollock diets resulting in equal energetic assimilation would require 56% more pollock than herring biomass (Rosen & Trites 2000). Together, these factors gave rise to the 'junk food hypthothesis' which attributes the Steller sea lion decline to consumption of nutritionally inadequate prey (Rosen & Trites 2000; Castellini 1993). Comparisons of prey quality, however, have been overly broad without sufficient regard for within species variability (Payne et al. 1999; Van Pelt et al. 1997; Worthy & Miculka 1997). Therefore, it is the purpose of this study to thoroughly examine the quality dynamics of several important species of Steller sea lion prey.

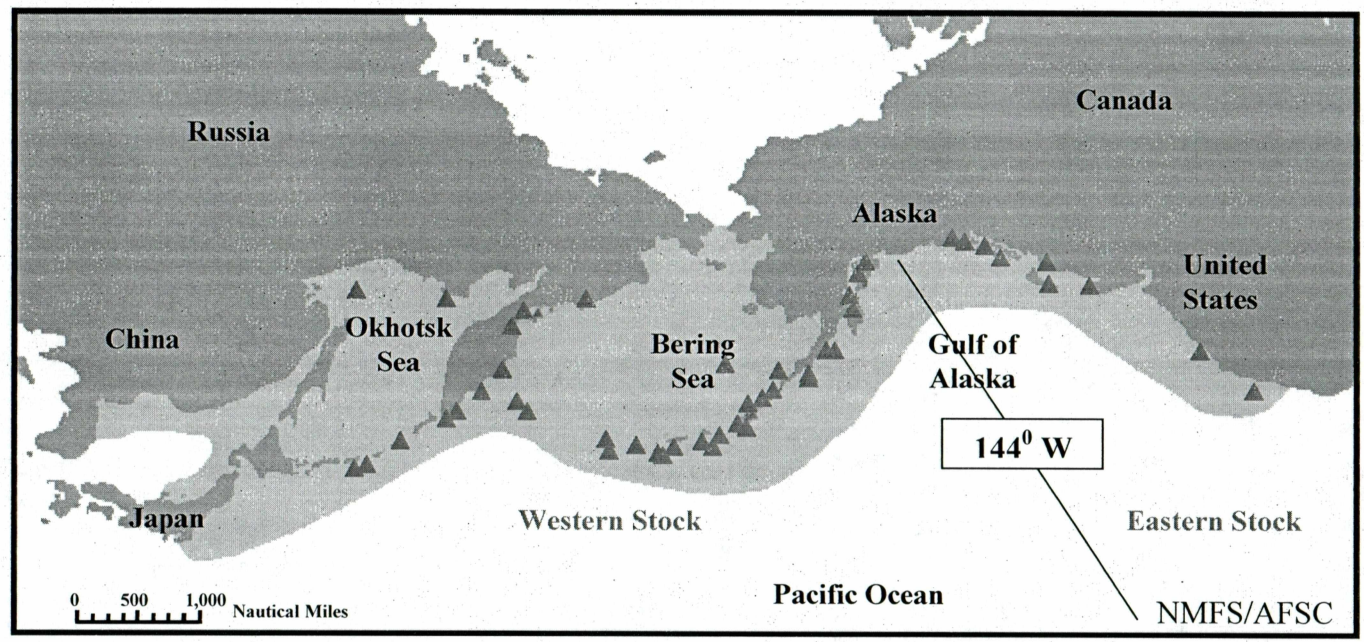

Figure 1.1. Steller sea lion (*Eumetopias jubatus)* range and stock divisions.
= Steller sea lion range, = Steller sea lion rookery

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CHAPTER 2

Variability in Steller sea lion (*Eumetopias jubatus*) prey quality in southeastern Alaska*

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ABSTRACT

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Though body composition of some fish species is known to be dynamic, few studies have systematically assessed the magnitude of these fluctuations with the exception of several single-species investigations. Analyses of fish body composition are often limited by non-systematic sampling designs and are restricted to a single sample collection or opportunistic collections pooled together, both of which fail to account for possible spatial, temporal, size and gender-related effects. Non-comparable collection techniques result in varying characterizations of fish body composition. We systematically examined the body whole-body energy content and proximate composition of two groundfish species; walleye pollock (*Theragra chalcogramma*) and Pacific hake (*Merluccius productus*), and three forage fish species; Pacific herring (*Clupea harengus*), eulachon (*Thaleichthys pacificus*), and capelin (*Mallotus villosus*). Within species, variability in energy content and proximate composition were primarily accounted for by season. Body composition cycled seasonally for all species, though more dramatically in forage fish, with peaks in energy and lipid content in fall and early winter. Energy and lipid content was generally higher in forage fish than groundfish while groundfish tended to have more water. Slight asynchrony in the seasonal cycles between species, however, resulted in similarities in body composition between forage fish and groundfish at times. Seasonal fluctuations in body composition elucidate alternate life history strategies of forage fish and groundfish. In addition, the dynamic body composition of fish has important consequences for piscivorous predators, which receive different nutrition from a single prey species depending on the time of year.

KEY WORDS: Forage fish, Groundfish, Proximate Composition, Energy Density, Seasonality, Energetic strategies

INTRODUCTION

The nutritional hypothesis postulates that recent declines in Steller sea lion populations are the consequence of a change in available prey from 'high-energy' forage fish to 'low-energy' groundfish. Two premises upon which the nutritional hypothesis is founded include: (1) forage fish are consistently superior quality prey items to groundfish prey, and (2) quality of a single prey species is consistent among individuals and over time. I tested these assertions through a systematic study of the magnitude of variability of Steller sea lion prey quality, as well as the factors influencing variability. Prey were sampled at two sites in southeastern Alaska to examine spatial effects. Prey species examined included walleye Pollock (*Theragra chalcogramma*), including young-of-the-year (YOY), juvenile, and mature pollock, Pacific herring (*Clupea harengus*), eulachon (*Thaleichthys pacificus*), capelin (*Mallotus villosus*), and Pacific hake (*Merluccius productus*). The pollock samples included three size classes, young-of-the-year (YOY), juveniles, and mature. Prey quality was assessed through whole-body energy content and proximal composition, including lipid, protein, moisture, ash, and carbohydrate content. Effects of species, season, ontogeny, size, gender, and location on prey quality were evaluated.

Based on their biochemical composition, forage fish typical of the pre-decline era have been characterized as 'lipid-rich' and thus 'energy rich' while groundfish typical of the predator decline-era were characterized as energy-poor (Iverson et al. 2002; Anthony et al. 2000; Payne et al. 1999; Robards et al. 1999; Paul et al. 1998b; Van Pelt et al. 1997;

Worthy & Miculka 1997; Perez 1994; Sidwell 1981; Stansby 1976). Captive feeding studies subsequently reported that groundfish-dominated diets were nutritionally inadequate for growth and reproduction (Donnelly et al. 2003; Rosen and Trites 2002; Calkins et al. 2000; Kirsch et al. 2000; Rosen and Trites 2000; Rosen and Trites 1999). I tested the implicit assumption that forage fish are consistently better quality prey than are groundfish.

Energy content and proximal composition of a few Steller sea lion prey have been studied extensively. Forage fish such as eulachon (*Thaleichtys pacificus*), Pacific herring (*Clupea pallasii*), and capelin (*Mallotus villosus*) are considered relatively lipid-rich while groundfish such as walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), and flatfish species are characterized as lipid-depleted (Iverson et al. 2002; Anthony et al. 2000; Payne et al. 1999; Robards et al. 1999; Paul et al. 1998b; Van Pelt et al. 1997; Worthy & Miculka 1997; Perez 1994; Sidwell 1981; Stansby 1976) (Appendix A). Characterizations of prey species vary among studies, however, largely resulting from non-comparable collection techniques. Samples are typically obtained in one of two ways: (1) from a single collection, representing a particular life stage, time of year (predominantly summer), and geographical location, or (2) from opportunistic collections of various-sized fish from multiple locations and time periods. Often, samples collected opportunistically are pooled together, failing to account for possible spatial, temporal, and size-related effects. Those studies which do examine seasonal, spatial, and size-related variability of opportunistically-collected samples are often

limited by small sample sizes resulting from a lack of *a priori* sampling design. Thus, mean body compositions in the literature generally represent a single moment in time or are gross averages confounded by multiple variables.

Fish body composition is dynamic (Iverson et al. 2002; Robards et al. 1999; Paul & Paul 1998; Paul et al. 1998a; Paul et al. 1998b; Jorgensen et al. 1997; Maartensson et al. 1996; Montevecchi & Piatt 1984; Winters 1970; MacCallum et al. 1969; Stansby 1945). For example, the lipid content of Newfoundland capelin fluctuates between 2% in the spring following spawning to over 20% in the fall (Jangaard 1974). Similarly, energy content of sandlance in Kachemak Bay, Alaska increases 31% after the spring bloom between February and June (Robards et al. 1999) while walleye pollock in Prince William Sound, Alaska, may fluctuate by as much as 30-100% (Paul et al. 1998b). In some cases, intraspecific differences in body composition may exceed interspecific differences (Robards et al. 1999; Hislop et al. 1991). Thus, it is misleading to rely on a constant value as an index for a species' body composition. As described by Stansby (1945), 'average composition is of only theoretical interest since actually individual fish will vary so widely from such average values'.

The large variability in body composition has important ramifications for predator bioenergetics which are either assessed directly through captive studies or indirectly using bioenergetic models. Bioenergetic modeling can only be as good as the component estimates in the models, including parameters such as population size, seasonal and spatial distribution, energy requirements, diet composition, and energy content of prey. With

respect to sea lions, measurements of many of these parameters have become increasingly more accurate with long-term monitoring and systematic studies. Dependable data are available for population size and distribution from annual Alaska-wide counts as well as small-scale regional studies (Loughlin et al. 1992; Sease et al. 2001). In addition, seasonal and regional dietary information derived from scat analyses is available (Trites et al. in press; Womble & Sigler 2004; Wynne 2003; Sinclair & Zeppelin 2002). One component which has been disregarded, however, is that of prey quality. Data for prey energy content have often been limited to commercially important species. Values often have been calculated from prey collected in the summer in either a single region or many regions lumped together, thus not accounting for spatial differences. Limitations of existing estimates of energy content have ramifications for bioenergetic models which have been found to be extremely sensitive to prey inputs. In a model quantifying harp seal (*Phoca groenlandica*) bioenergetics, consumption estimates varied by 25% due to variability in model inputs (Shelton et al. 1997). Of the model parameters, which included species composition, assimilation efficiency and prey energy content, prey quality was found to be the most sensitive parameter causing changes in consumption values of up to 25%. It is therefore particularly important to have reliable estimates for these parameters.

METHODS

Sampling

Prey samples were collected in southeastern Alaska within a 45 km radius of two sites occupied by Steller sea lions, Benjamin Island in Lynn Canal and the Brothers Islands in Frederick Sound (Figure 1). Approximately 750 animals use Benjamin Island in winter and about 1,200 animals are present year-round in Frederick Sound (Womble 2003). The study sites were assumed to be foraging areas for sea lions on the haulouts based on telemetry data which suggests that sea lions generally make relatively short foraging trips (>20 km from the haulout) (Raum-Suryan et al. in press; Loughlin et al. 2003). In addition, otariid life history strategy necessitates that sea lions forage in the vicinity of their haulouts as mothers return to the haulout to nurse their pups between foraging bouts and later accompany the more developed juveniles on foraging bouts of their own (Costa 1991).

Specimens were collected during quarterly acoustic trawl surveys in May, September, December and March of 2001 and 2002. Trawl surveys followed box transects within 45 km of two study sites. Fish schools were identified and targeted based on hydroacoustics sampling with a hull-mounted 38 kHz Simrad EK60 echo-integration system with a 12° beam angle. The echosounder transducer was operated at 11 $km \cdot h^{-1}$. Location data from a global positioning system (GPS) were collected simultaneously. Targeted prey were collected using mid-water rope trawls from chartered fishing vessels. In 2002, the mid-water trawl was a 164 Nordic rope trawl with

1.5 m^2 alloy doors, 7 m height and 17 m width with a 19 mm mesh codend liner. The midwater trawl was larger in 2003 to match the larger vessel and trawl-handling equipment used that year. In 2003, the mid-water trawl was a mesh wing 25/21/64 trawl with 3 m^2 alloy doors, 11 m height and 29 m width with a 32 mm mesh codend liner.

Prey Selection

Species selected for analysis were among those that predominanated in seasonal scat data collected from the two study sites (Figure 2) (Trites et al. in press; Womble & Sigler 2004). In addition, selected species were also among the most abundant species as determined by preliminary results of concurrent acoustical biomass surveys (M. Sigler Auke Bay Lab, NOAA Fisheries, US Dept Commerce, 11305 Glacier Hwy Juneau, AK personal communication). Species were limited to those accessible by trawl, however, which precludes the analysis of some other important prey items such as skate, salmon and flatfish. To examine size-related differences in body composition, individuals of a species were collected across all sizes present (Table 1). To capture gender related effects, equal numbers of males and females were selected. Sample sizes of ten animals of each species were collected during each sampling period. All species were not abundant during each season, however, resulting in some smaller sample sizes. Thus, supplemental samples were sometimes collected from intermediate time periods.

Sample Preparation

To ensure the chemical integrity of samples, fish were frozen immediately after measuring fork length and total body weight as well as determining gender. Fish were

flash frozen in refrigerated liquid nitrogen (–196° C) and packaged using a vacuum sealer or tightly-wrapped cellophane. In the absence of liquid nitrogen, fish were packaged and placed in a single layer on refrigerated shelves of a –20 °C commercial-grade freezer. Upon return to the laboratory, specimens were transferred to a –80 °C freezer or a -20 °C overflow walk-in freezer for storage until they could be analyzed within three months.

Several days before analyses, whole fish were homogenized while frozen. Small fish were combined into composites of several similarly-sized fish to obtain large enough sample sizes for analyses (>6g). Small fish were homogenized into a uniformly colored puree using a Tekmar Tissumizer. Large fish were sliced into small pieces approximately 4 cm thick using a Bizerba FK23 meat band. Pieces were subsequently homogenized using a Fleetwood M12S meat grinder with a 4.5 mm die. The resultant homogenate was mixed by hand and reground two additional times with successively smaller dies to produce a course homogenate. A random sample was selected and pureed further in a Cuisinart food processor until a uniform color and consistency were achieved. Prior to sample storage, the temperature of the homogenate was measured to ensure that the sample was still frozen. Sample aliquots were randomly chosen, placed in storage vials topped with nitrogen gas, and were maintained in a –80 °C freezer prior to analysis.

Energy Content

Energy densities can be measured directly through bomb calorimetry or calculated indirectly as the sum of the energy content contributed by the total-body lipid, protein, and carbohydrate proximate fractions. Energy densities determined by the two methods

are found to be similar when the correct energy equivalents are used (Hislop et al. 1991; Craig et al. 1978). Agreement of the two methods was validated in the present study using a subset of samples (n=17) in which calculated energy densities were compared to bomb calorimetry measurements for both relatively high- (Pacific herring) and low- (walleye pollock) energy prey species. Bomb calorimeter measurements of energy content were calculated as the mean of two replicate samples of dried fish homogenate pellets of approximately 0.15 g in replicate in a Parr 1425 Semi-micro bomb calorimeter. For comparison, energy densities were calculated from proximal composition using the subsequently-described energy equivalents. Energy contents from the two methods were compared using straight line regression. The slope of the regression was tested for inequality to 1.

A range of energy equivalents exist for the conversion of proximate composition to energy content, and the equivalents of 36.43 $kJ \cdot g^{-1}$, 20.10 $kJ \cdot g^{-1}$, (Brett 1995), and 17.17 $kJ \cdot g^{-1}$(Anthony et al. 2000; Van Pelt et al. 1997; Brett 1995) were selected for this study for lipid, protein and carbohydrate, respectively (Appendix 2.1). Energy contents were expressed on a relative mass basis ($kJ \cdot g^{-1}$) for comparison among different species and sizes of fish as well as comparison with other studies.

Lipid

Lipid was extracted using a modification of Folch's method outlined by Christie (1989) using a Dionex Accelerated Solvent Extractor (ASE) 200. Approximately 1 g of wet sample homogenate was mixed with a drying agent (Hydromatrix) and masticating

agent (sand) and loaded into ASE cells. Samples were extracted using a 2:1 (v:v) chloroform:methanol solvent at 1200 psi and 120 °C. Following extraction, the filtrate was washed to remove the coextractables with a 0.88% KCl solution followed by a solution of 1:1 (v:v) methanol:deionized water, both in a volume equal to 25% of the extract volume. Excess solvent was evaporated using a Yamato BM400 water bath to reduce the sample to 1 ml. Percent lipid was calculated gravimetrically by sacrificing 0.5 ml of lipid-solvent solution and evaporating the solvent to dryness. Quality assurance samples extracted with each batch of 17 samples includes: (1) a blank, (2) a replicate sample consisting of a second aliquot of homogenate of one of the samples in the batch, and (3) a reference sample of herring homogenate which has been previously characterized for proximate composition.

Protein

Protein content was estimated by multiplying total nitrogen content by a conversion factor of 6.06 (Jones 1931) to account for the nitrogen content of protein (Leco Instruction Manual 2001; Craig et al. 1978) (Appendix 2.2). Nitrogen content was measured with a LECO nitrogen analyzer FP 528 following the Dumas method (Association of Official Analytical Chemists, 2002). Samples of approximately 0.1 g of dried homogenate crushed into a fine powder were wrapped in foil with excess air squeezed out. Samples were then combusted in a chamber at 850 °C from which nitrogenous gases were expelled and quantified. Samples were replicated, and if the difference of the replicates exceeded 1 standard deviation, samples were reanalyzed.

Quality assurance samples included with each batch of 17 samples were (1) a blank reference sample of pure cane sugar, and (2) a reference walleye pollock homogenate calibrated to a National Institute of Standards and Technology (NIST) Standard Reference Material (SRM). Additionally, the instrument was calibrated daily with EDTA samples.

Carbohydrate

Fish do not store carbohydrates in significant amounts as energy reserves (Brett 1995), and thus carbohydrates are considered negligible in fish and are disregarded in many bioenergetic studies (Montevecchi & Piatt 1984; Sidwell 1981; Craig et al. 1978; Stansby 1976; Stansby 1945). I validated this assumption by examining the effect of carbohydrate content on the calculated energy content. Carbohydrate content of individual fish was calculated using the commonly-used subtraction method, assuming that the majority of animal composition is restricted to lipid, protein, water, ash, and carbohydrate (Robbins 1993; Watt and Merrill 1963; Brody 1945):

$$\text{Carbohydrate Content (\%)} = 100\% - \text{Lipid Content (\%)} - \text{Protein Content (\%)} - \text{Moisture Content (\%)} - \text{Ash Content (\%)}$$

Energy contributed by carbohydrates was then calculated by multiplying the energy equivalent of 17.17 $kJ \cdot g^{-1}$ by the carbohydrate mass. If calculated carbohydrate contents were too small to change the energy content by at least one standard deviation, the possible effects of carbohydrates were ignored.

Moisture and Ash

Initially, moisture content was measured gravimetrically by drying ~4g of the sample homogenate in a 75 ^{o}C drying oven until a constant weight was achieved. After

calculating percent moisture, samples were ground to a fine powder and used for ash analyses. Ash content was measured by incinerating a portion of the dried homogenate in pre-muffled ceramic crucibles in a muffle furnace at 550 °C for 12 hours. Quality assurance samples for both moisture and ash included blanks and duplicates. After the September 2002 sampling date, a Leco Thermogravimetric Analyzer (TGA) 601 was purchased and moisture and ash contents were measured using the new instrument. Moisture and ash values obtained from the two methods varied by less than 1%. The TGA measures moisture and ash content gravimetrically using a ramping temperature regime. Samples were placed in ceramic crucibles and brought to a temperature of 135 °C, which was maintained until a constant sample mass was achieved from which moisture content was calculated. Immediately following, the temperature was ramped to 600 °C and maintained until constant masses were achieved from which ash content was calculated. Quality assurance samples for moisture and ash analysis included with each run were blanks and reference pollock homogenate calibrated to the National Institute of Standards and Technology (NIST) standard reference material (SRM) 1946.

Statistical Analysis

Statistical analyses were performed on a wet mass basis to facilitate comparisons with prey items. Bomb calorimetry and calculated estimates of energy content were compared using straight-line regression analysis. Summary statistics were calculated for energy content and proximal composition for comparison to other studies. Proximal composition and energy content data were tested for compliance with ANOVA

assumptions using the Anderson-Darling test for normality and Levene's test for homoscedasticity. These data failed to meet the assumptions and were arcsin transformed. General linear models with Tukey pairwise comparisons tested for possible effects of season and gender on fish body composition. Two sample t-tests tested for spatial differences in body composition. Linear regression was used to understand the relationships between continuous morphometrics characters and body composition.

RESULTS

Negligibility of Carbohydrate Content

The carbohydrate content required to have an effect on energy content by exceeding error associated with lipid and protein analyses was never smaller than 4.37% of the fish biomass. Due to the relatively small carbohydrate content, as the lipid content of fish increased, the carbohydrate content required to affect the energy content increased. In the most lipid-rich fish, the minimal carbohydrate content required to have an have an effect on the energy content was 21.05%. In contrast, the calculated carbohydrate content averaged only 0.03%, ranging from-9.72 to 11.22% (negative values were illustrative of cumulative error in the analyses of the other proximal fractions). The calculated carbohydrate content was large enough to significantly influence energy content for only one fish, a male herring collected in June of 2002 (the calculated value was 8.21% while the value to affect energy content was 5.04%). As

carbohydrate content was generally found to be negligible, it was ignored in all further analyses.

Calculated Energy Content

Energy contents as estimated by calculation and measured by bomb calorimetry methods were highly correlated (r^2=0.94) (Figure 3). The regression slope was no different than 1 (t=0.975, df=15, α=0.05). Thus, calculated energy densities were considered an accurate estimate of energy content.

Overall Prey Quality Variation

Prey quality of 942 fish was examined. Mean energy content and proximal composition was intermediate with respect to previously published ranges for fish in the northern Pacific Ocean with the exception of hake, for which only one previous study of whole body composition could be found (Table 3). The single published observation of hake composition, which was lower in lipid and energy content than fish from this study, is from an unknown location and could have been collected anywhere in its range from Baja California to the Aleutian Islands, Alaska (Mecklenburg et al. 2002; Eschmeyer & Herald 1983).

Energy content of fish was influenced by lipid more than protein as a result of the relatively large magnitude of lipid's energy coefficient as well as the large variability of lipid content among individuals. Energy content of species with more than approximately 10% lipid was derived primarily from lipid while energy content of species with less than 10% lipid was derived primarily from protein (Figure 4).

Energy content and proximal composition varied considerably among and within species, causing significant overlap across species such that no one species was consistently the best source of any nutrient (Figure 5). Lipid content varied more than other proximal fraction. Though moisture varied inversely to lipid, the large magnitude of moisture content caused the relative changes to be small. For example, the maximal lipid content of a eulachon (28.85%) was 289 times the minimal lipid content of a mature pollock (0.10%). Within species, lipid content varied on average 40 times among minimal and maximal values. Pollock had the most variable lipid content, with individuals varying by greater than two orders of magnitude (0.10% - 11.06% lipid). Other proximal fractions varied considerably less; ash content varied on average 2.9 times among minimal and maximal values within species, followed by energy content (2.8 times), protein content (1.7 times), and moisture content (1.2 times). Herring had the most dynamic body compositions, varying more than other species in protein, moisture, and energy content. Ash content was most variable among pollock.

In general, eulachon and herring were similar to each other in energy, lipid, and moisture content, but distinct from the other species, while capelin and hake tended to be similar in all respects (Figure 5). Hake overlapped with pollock, and all three sizes of pollock were similar in composition. Moisture content was less variable among species and only 3 groups could be discriminated. In general, eulachon tended to have the highest energy and lipid content, followed by herring, hake, capelin, mature, juvenile and YOY pollock. The opposite trend was observed for moisture content due to an inverse

correlation between moisture and lipid content ($r^2 = 0.85$) as well as moisture and energy content ($r^2 = 0.92$). Protein content tended to be highest in herring, followed by mature, juvenile, and YOY pollock, capelin, hake, and eulachon. Ash content was generally greatest in mature pollock.

Seasonal Effects

Seasonal effects accounted for much of the within-species variability in body composition. In particular, energy, lipid, and moisture content fluctuated the most between seasons, following the trend of a single rise and fall over the period of a year (Figures 7-11). In nearly all cases, energy and lipid content peaked in September or December, falling to a minimum in the spring. Seasonal trends were slightly out of phase among species, particularly eulachon, herring, and capelin, with maxima occurring at adjacent sampling periods. Seasonal asynchrony between species caused the relative ranking of prey by body composition to fluctuate throughout the year such that no one species remained the best source of energy, lipid, or moisture content. Eulachon and herring had consistently higher energy and lipid content than pollock and hake, however, and were usually considerably higher. Trends in hake and pollock energy, lipid and moisture content were more synchronous.

Seasonal changes in protein content were less regular and predictable than that of energy, lipid, and moisture, with no consistent pattern observed for all species (Figure 9). In addition, patterns in protein content were dissimilar between years for all species except eulachon, which peaked in the winter and reached minima in the spring during

both years. In general, herring tended to have the highest protein content year-round, followed by pollock and capelin (which often overlapped), and hake and eulachon. Seasonal changes in ash content were similarly irregular, following no similar patterns among species or between years (Figure 11). Ash content was greatest in pollock, followed by herring, hake, and capelin (which overlapped significantly throughout the study period), and eulachon.

Interannual Effects

Interannual differences in energy content and proximate composition were minimal (Figures 6-10). Of energy content and proximal composition, protein content varied the most between years, with differences occurring primarily between May of 2001 and 2002. Among species, herring and pollock had the greatest degree of interannual variability in body composition. These differences were not limited to a single proximate fraction. The proximate composition of herring varied primarily between September 2001 and 2002. Interannual differences in pollock composition were not limited to a single month.

Ontogenetic Effects

Ontogenetic differences in body composition were assessed for pollock for which three age classes could be most consistently sampled throughout the study period (Figures 7B-11B). The three age classes of pollock tended to have similar body compositions, with juveniles having values intermediate to mature and YOY fish. For approximately 30% of the observations, all age classes were statistically similar, while

another 40% of the time, matures and juveniles were statistically similar. For the remaining observations, juveniles and YOY fish were similar. Only on two instances were values of body composition of mature fish statistically similar with that of YOY and to the exclusion of juveniles. Both instances involved ash content.

All size classes of fish tended to follow similar seasonal patterns. Mature pollock showed the greatest magnitude of variability. As found previously for all species, asynchronicity in seasonal patterns caused similarities among age groups, particularly between mature fish and juveniles.

Fish size expressed as length or weight correlated weakly with energy content proximal composition ($r^2 < 0.28$ for all correlations). Size associations between moisture ($r^2 < 0.15$) and ash content ($r^2 < 0.08$) were negative. Correlations within season were apparent, though not consistent among seasons.

Spatial Effects

Analysis of spatial differences in proximal composition between Frederick Sound (FS) and Lynn Canal (LC) were limited to juvenile pollock, mature pollock, and herring due to sample availability. Spatial differences occurred inconsistently, explaining little variability in body composition. Across all seasons, only juvenile pollock had consistent differences in body composition between study sites. Energy (FS=4.26$\pm$0.70, LC=3.95$\pm$0.48; P=0.002) and protein (FS=15.28$\pm$1.29, LC=14.58$\pm$1.19; P<0.001) contents of juvenile pollock were significantly greater in Frederick Sound than in Lynn Canal while moisture content was higher in Lynn Canal (FS=78.64$\pm$1.83,

LC=80.03±1.49; P<0.000). Within collection periods, spatial differences were primarily limited to September and December.

Gender Effects

Gender had a minor influence on the body composition of prey species. Across all seasons, only herring protein (♀=15.50±1.11, ♂=16.11±0.97; P=0.002) and ash (♀=2.30±0.37, ♂=2.67±0.45; P<0.000) contents differed among genders, with males having greater percentages of each. Within seasons, further discrepancies between the sexes occurred, primarily in December and March.

DISCUSSION

Mean proximal composition and energy content of fish in the present study were intermediate to values previously documented in the literature for fish in the North Pacific Ocean, though ranges observed in this study exceeded those previously reported (Anthony et al. 2000; Anthony & Roby 1997; Bando 2002; Foy and Paul 1999; Harris et al. 1986; Iverson et al. 2002; Paul and Paul 1998; Paul et al. 1998a; Paul et al. 1998b; Payne et al. 1999; Perez 1994; Sidwell 1981; Stansby 1976; Van Pelt et al. 1997; Worthy & Miculka 1997). Variability in body composition was greater than previously reported, likely due to the short sampling periods or pooled samples in previous studies, which obscured the strong seasonal pattern revealed here. Within-species variability resulted in a high degree of similarity in body composition among species. For a given species, lipid content and consequently energy content were the proximal fractions that varied the greatest. Within a

species, lipid content varied by an average of 35-fold among individuals, with over 100-fold differences among individual mature pollock. Due to lipid's utility as an energy reserve, it is prone to large fluctuations, particularly in poikilothermic animals (Robbins 1993; Schmidt-Nielsen 1990). In fish, energy is drawn from lipid reserves until a critical low lipid content is reached after which protein is utilized (Love 1974).

Of the factors examined, seasonal effects were the primary source of fluctuations in energy content and the proximate fractions. Seasonal variation does not imply a single cause, however, as season is a broad descriptor, encompassing many factors including environmental effects, dietary shifts, and the seasonality of maturity and spawning (Love 1974). Results agree with findings in other studies, in which the fish that exhibit the greatest seasonal changes in body composition are mature individuals of a species capable of large fat deposits as well as those that spawn in the spring. Such fish typically show a pattern of increasing fat deposits over the summer as a result of intense feeding activity. Peak condition is achieved in the fall or winter, then condition declines precipitously in the early spring due to scarce food supplies and the energetic demands of spawning. Energetic minima occur just prior to or immediately after spawning (Iverson et al. 2002; Jorgensen et al. 1997; Maartensson et al. 1996; MacCallum et al. 1969; Montevecchi & Piatt 1984; Paul & Paul 1998; Paul et al. 1998a; Paul et al. 1998b; Robards et al. 1999; Stansby 1945; Winters 1970). Eulachon and capelin were collected in this study from spawning aggregations in April, the time during which these species reached energetic minima. Local herring stocks spawn in late April and May (Carlson 1980), perhaps

explaining the relative delay in herring energetic minimum. Depletions of lipid and protein stores can be attributed to gonad development as well as starvation, which may occur in combination in some species such as Pacific herring which cease to feed during gonad development (Love 1974; McBride et al. 1960).

Relatively small ontogenetic differences in energy content and proximal composition probably result from alternate strategies employed by different age classes of fish. Predation pressure is the greatest threat to small fish, thus causing younger animals to allocate the bulk of their energy to growth. Upon reaching larger sizes, predation pressure diminishes and is replaced by a lack of food supplies as the major threat to survival (Parker 1971). The results of this study demonstrate that mature fish have greater energy reserves than juveniles. Large energy densities are required by older fish which are more fecund, making relatively greater demands on their resources (Love 1974). Furthermore, most fish species become more fecund with age, creating a demand for greater energy reserves. Though differences occurred among ontogenetic classifications, only weak correlations with body composition and length or weight of the fish were found. Similar seemingly contradictory findings have been observed in other studies (Anthony et al. 2000; Iverson et al. 2002; Maartensson et al. 1996; Paul & Paul 1998; Paul et al. 1998a; Van Pelt et al. 1997; Winters 1970). Observation suggests that differences in body composition are more a result of sexual maturity than size (Love 1974).

Gender had minimal effect on fish body composition, similar to other studies (Paul et al. 1998a), except near the spawning season when gender differences were maximized. During the remainder of the year, energy allocation strategies of the two genders were similar and their body compositions are the same. Similar results have been found for other fish, with females having greater fluctuations in body composition as a result of the greater energetic demands imposed by spawning (Love 1974).

Geographical differences were insignificant on the spatial scale of 160 km examined in this study. The locations chosen for spatial comparison, though relatively close, differ by freshwater input systems as well as different passages to open ocean. Different body compositions of fish might have been expected due to potential differences in productivity, particularly since differences have been observed on scales as small as within Prince William Sound, Alaska (Iverson 2002).

Interannual differences in body composition between May 2001 and May 2002 suggest that fish condition may be directly linked to differences in environmental fluctuations and spring primary productivity blooms. This time of minimal energy reserves may a critical low point from which fish must build adequate energy supplies for overwinter survival (Sogard & Olla 2000) and subsequent spring spawning success (Madenjian et al. 1996). Minimal and maximal energy reserves have been suggested as a useful index for forecasting fish recruitment (Marshall et al. 2000).

The relatively large fluctuations in proximate composition have important ramifications for piscivorous predators, which may experience large differences in nutrient

content of a single species depending on the time of year they are consumed. Little information is available regarding prey selection of Steller sea lions. They are considered opportunistic samplers of the environment, consuming fish that are readily available (Trites 1998; Sinclair et al. 1994). Sea lion diet composition is significantly influenced by region and season. Plasticity in diet allows animals to take advantage of seasonally abundant aggregations of fish (Womble & Sigler 2004; Sinclair & Zeppelin 2002). Seasonal, ephemeral prey aggregations such as eulachon and herring spawns, as well as overwintering herring schools are considered a major factor in prey selection by sea lions (Womble 2003). Thus, seasonal variation in prey body composition should be combined with seasonal foraging habits to assess sea lion bioenergetics.

This study provides prey quality data for Steller sea lions in southeastern Alaska, a region in which populations are increasing. Comparison to prey quality in the western, declining stock should be made. In addition, future study should seek to refine several coefficients routinely used in bioenergetic studies, including energy equivalents and a conversion factor for nitrogen to protein content. These coefficients have been developed for terrestrial animals and should be defined for extension to the marine environment in which differences in fatty acid and amino acid content are likely to have substantial effects (Robbins 1993; Henderson & Tocher 1987).

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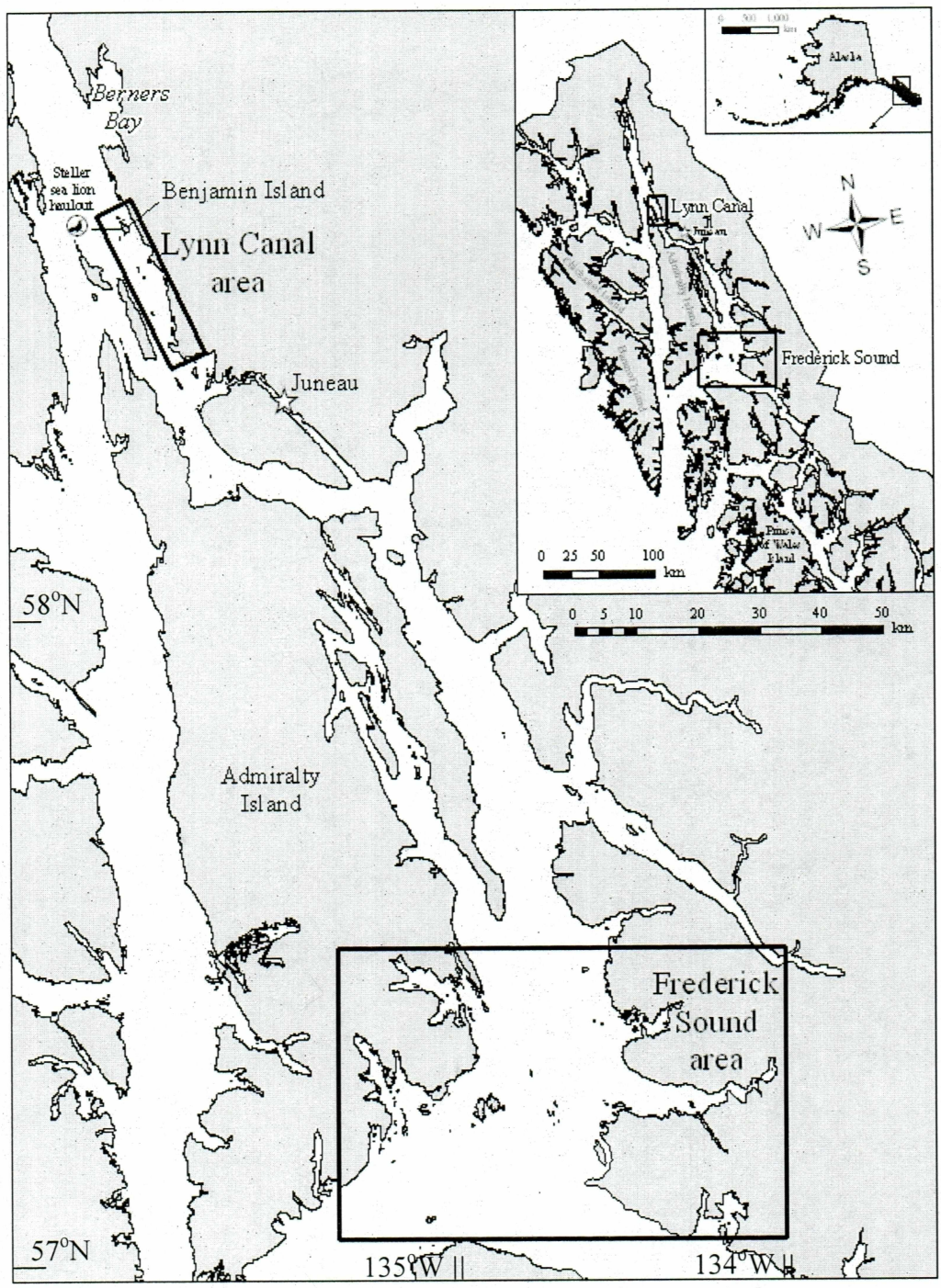

Figure 2.1. Study sites.

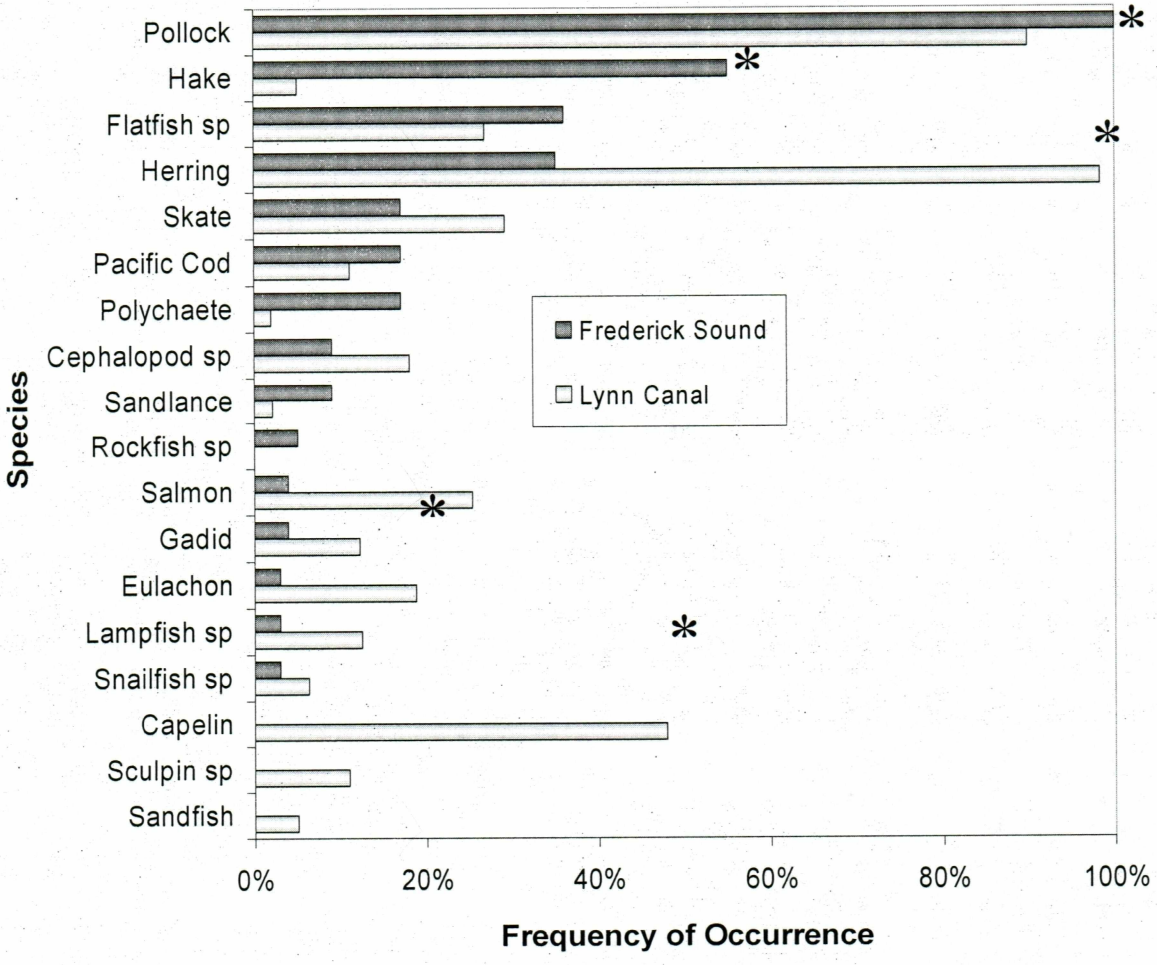

Figure 2.2. Steller sea lion (*Eumetopias jubatus*) diet inferred from hard part analysis of scats. Scats were collected from Benjamin Island haulout and Frederick Sound haulouts in southeastern Alaska. Data are expressed as frequency of occurrence. Prey species depicted are those represented in ≥5% of the scats (J. Womble unpublished data; Trites et al. in press). Species selected for analysis in this study are indicated with an asterisk.

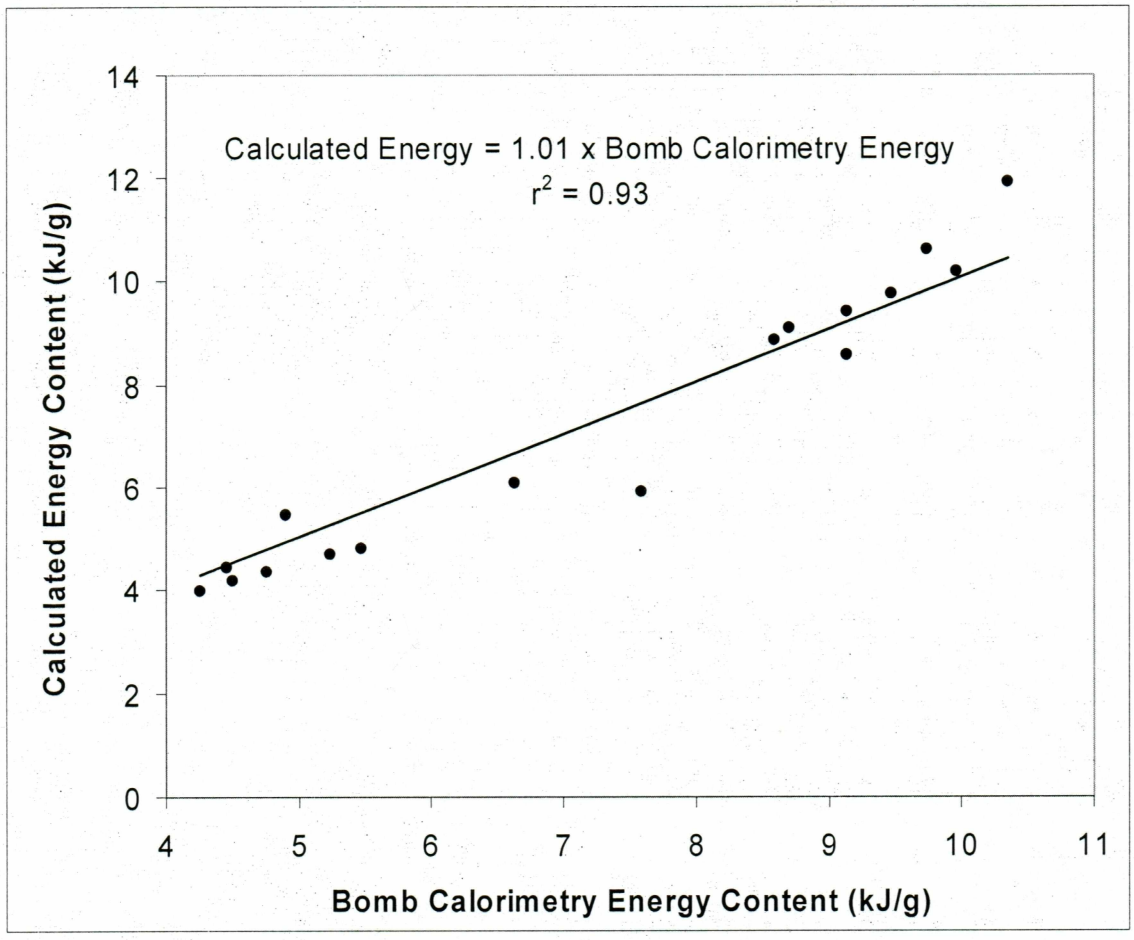

Figure 2.3. Comparison of energy content estimated by calculation versus bomb calorimetry measurements. The slope of the regression line is no different than 1, as determined with hypothesis testing using a t distribution ($t=0.975$, $df=15$, $p< 0.05$).

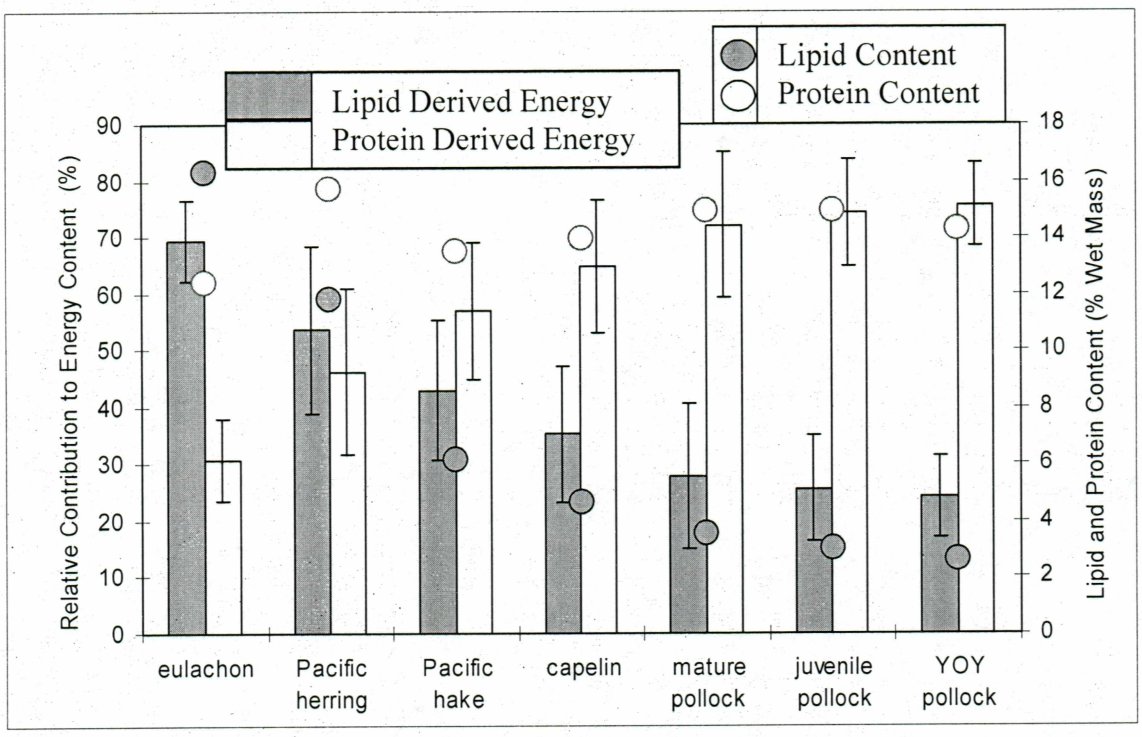

Figure 2.4. Proportion of energy (%) in fish derived from lipid and protein.

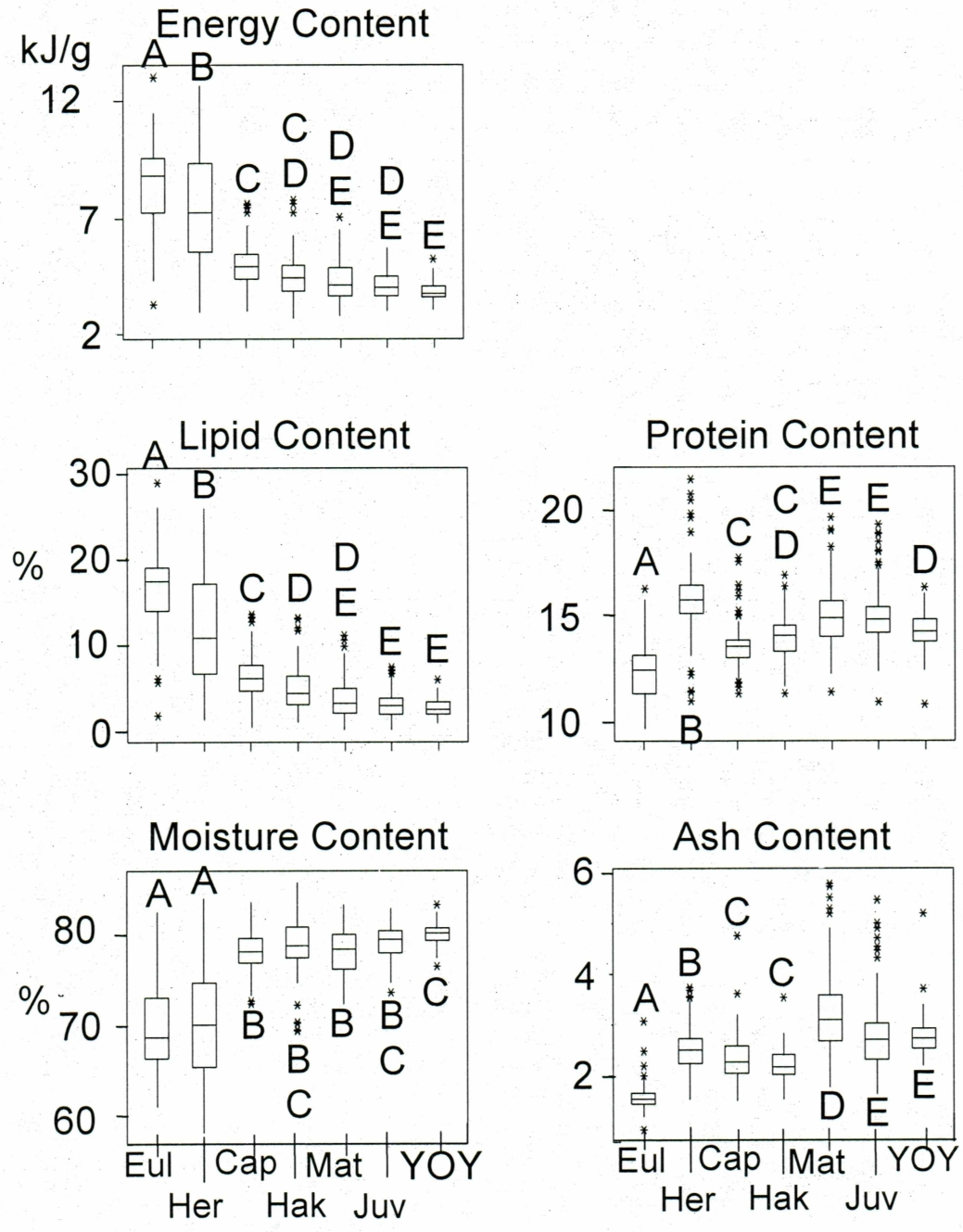

Figure 2.5. Interquartile range boxplot of fish energy content ($kJ \cdot g^{-1}$) and proximate composition (relative percents) on a wet mass basis. Letters represent statistically similar species periods as determined by ANOVA using Tukey's pairwise tests corrected for multiple comparisons ($p<0.05$).

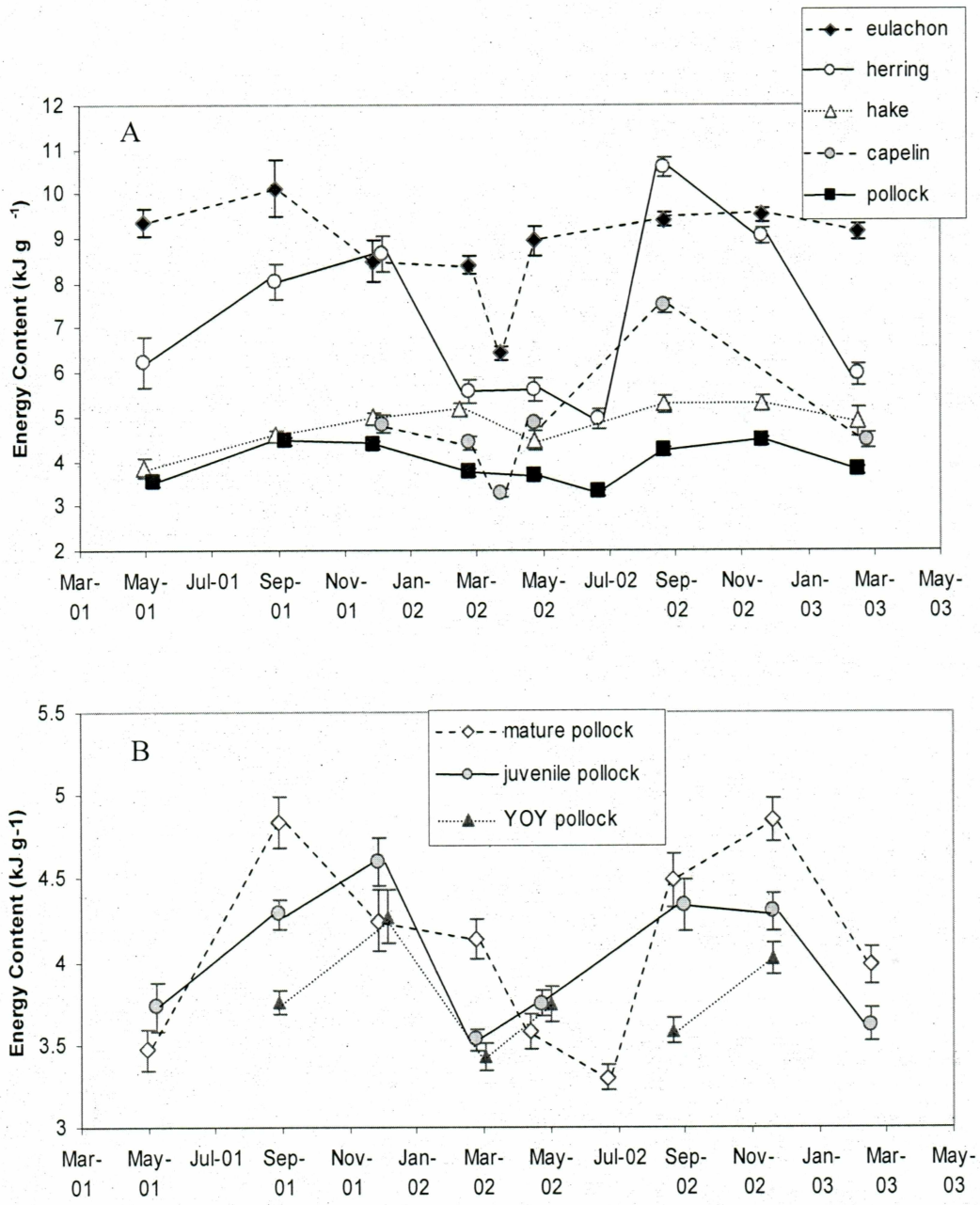

Figure 2.6. Seasonal whole-body energy content of fish (± one standard error). Panel A depicts all species and panel B depicts pollock by age class.

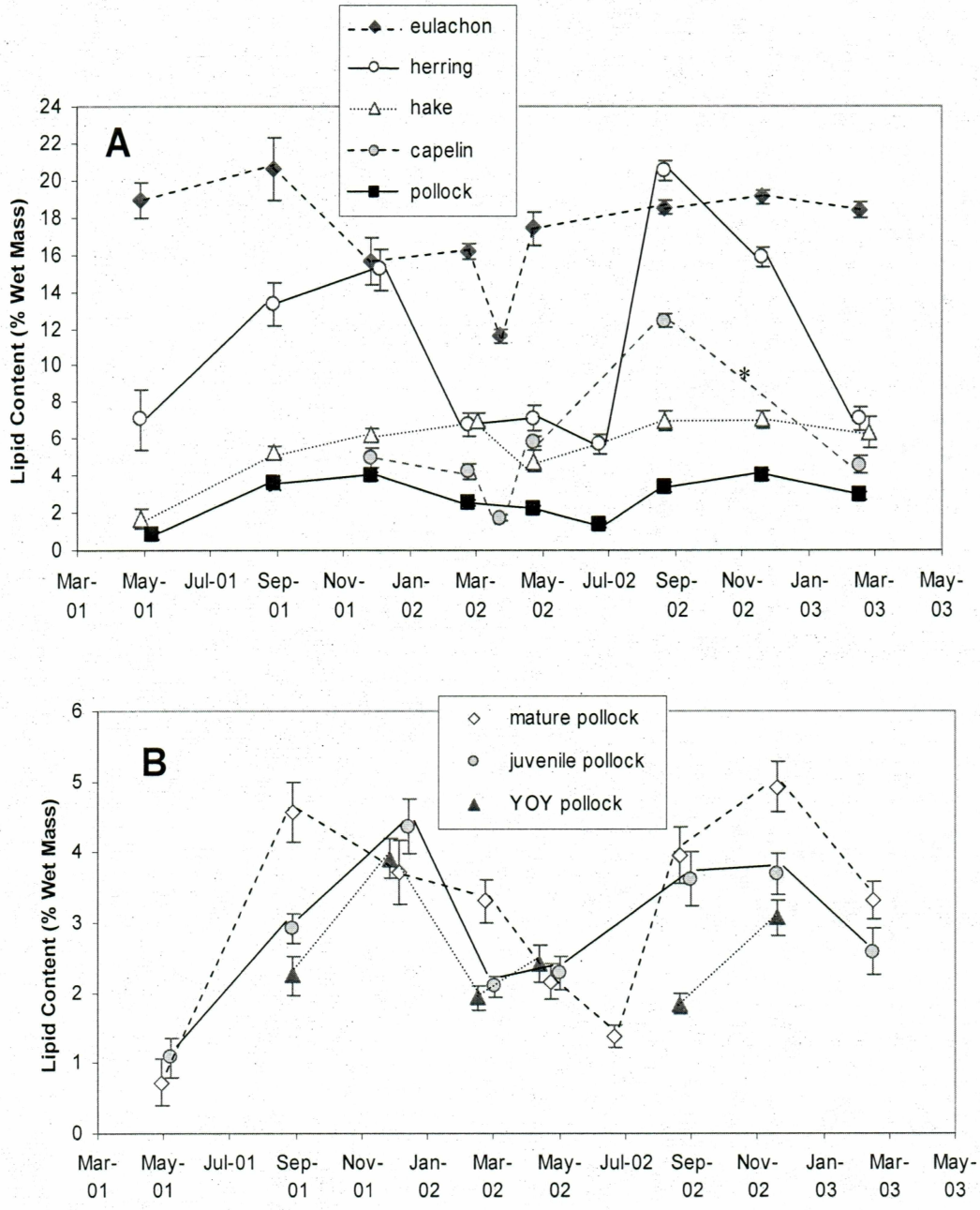

Figure 2.7. Seasonal whole-body lipid content of fish (± one standard error). Panel A depicts all species and panel B depicts pollock by age class.

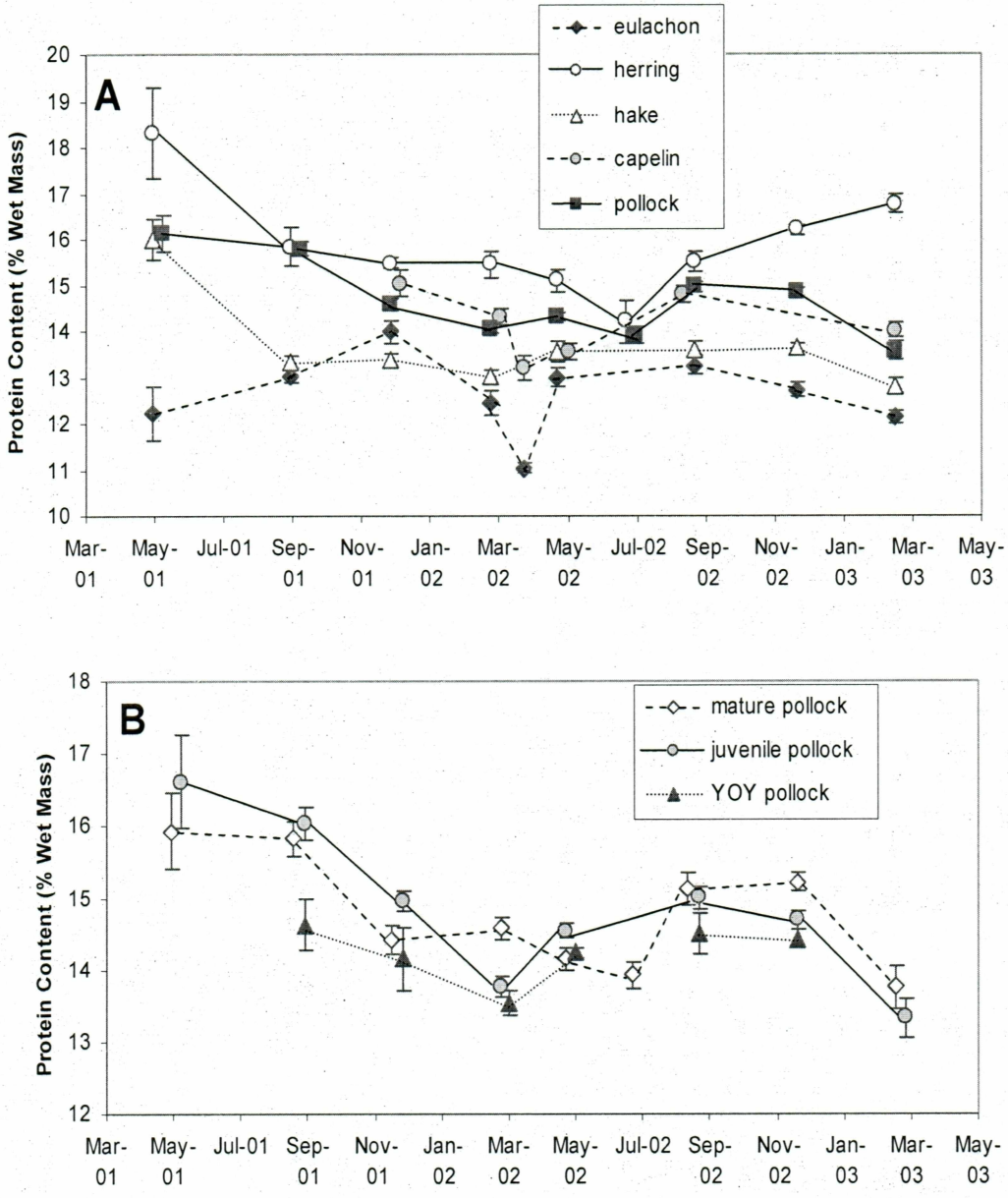

Figure 2.8. Seasonal whole-body protein content of fish (± one standard error). Panel A depicts all species and panel B depicts pollock by age class.

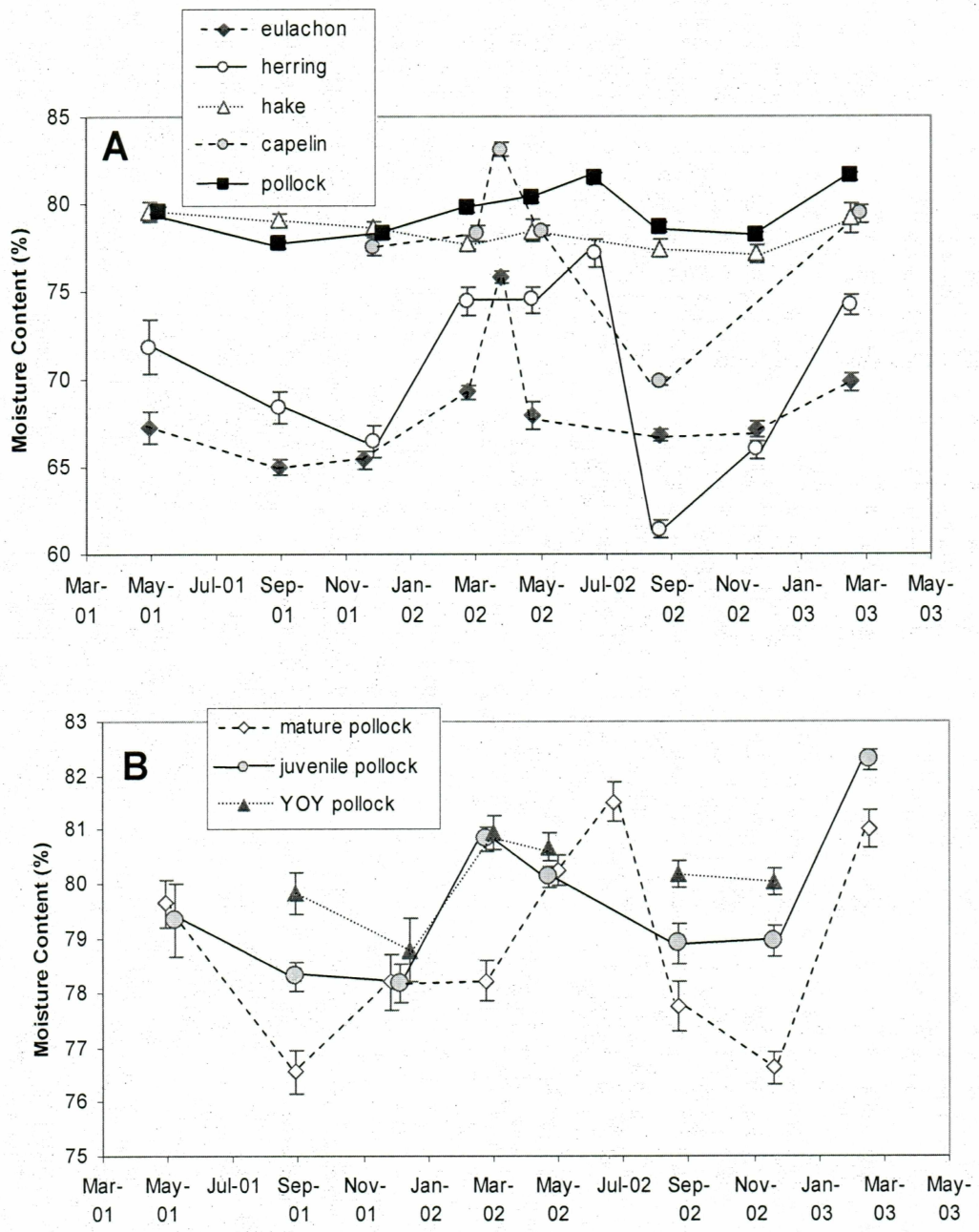

Figure 2.9. Seasonal whole-body moisture content of fish (± one standard error). Panel A depicts all species and panel B depicts pollock by age class.

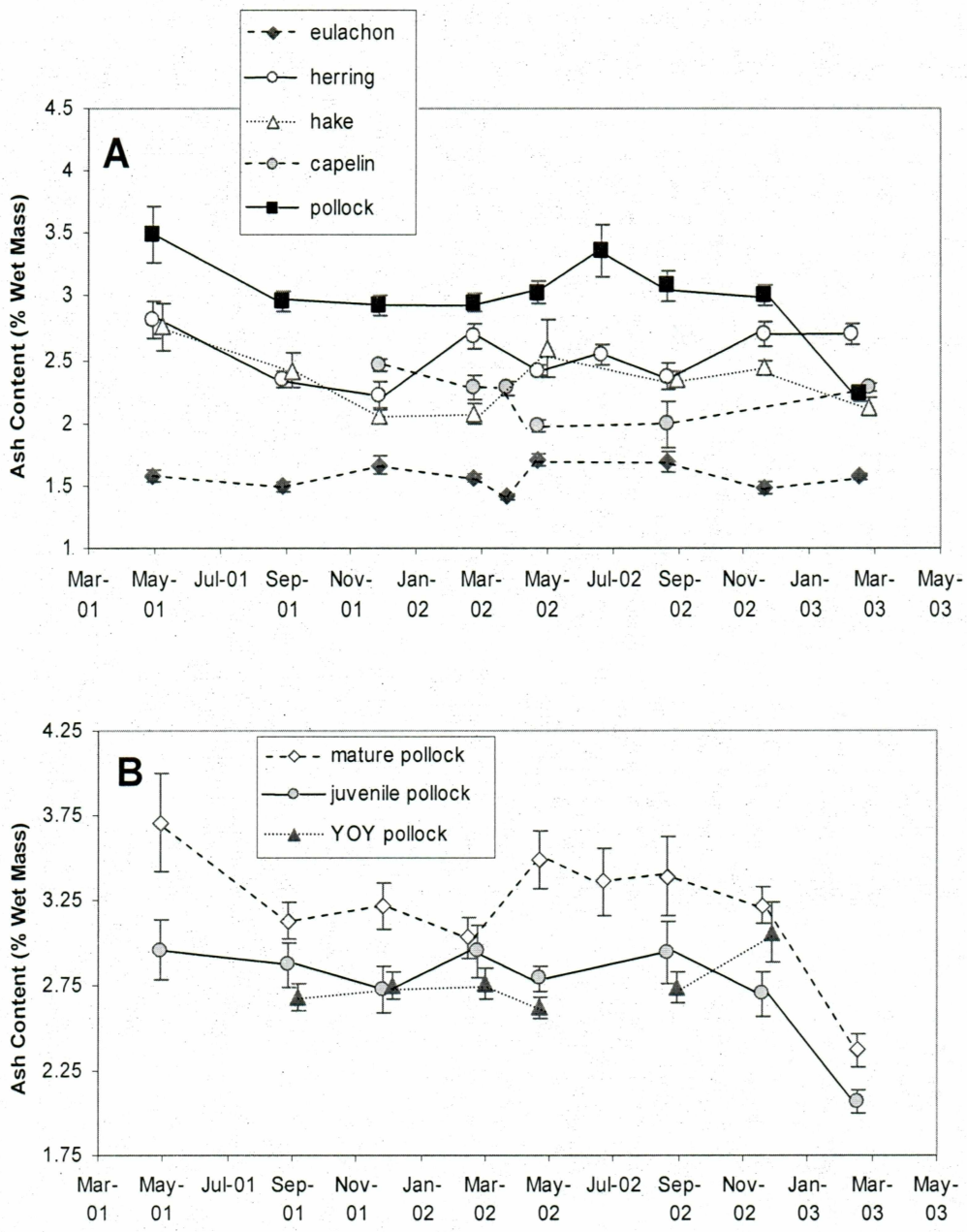

Figure 2.10. Seasonal whole-body ash content of fish (± one standard error). Panel A depicts all species and panel B depicts pollock by age class.

Table 2.1. Size ranges of fish from trawl surveys and mean sizes of fish sampled. Sizes are expressed as fork length ± one standard deviation.

Species	Range of Fork Lengths (mm) of Fish in Trawl Surveys	Mean Fork Length (mm) of Sampled Fish	Mean Mass (g) of Sampled Fish
Eulachon	97-224	166.6 ± 28.2	33 ± 17
Herring	75-280	188.1 ± 45.8	83 ± 55
Capelin	70-140	107.1 ± 15.0	8 ± 4
Hake	200-660	487.9 ± 66.7	855 ± 38
Mature Pollock	290-668	472.9 ± 73.6	894 ± 427
Juvenile Pollock	110-380	248.0 ± 65.3	139 ± 102
YOY Pollock	70-180	119.7 ± 24.2	13 ± 8

Table 2.2. Comparison of body composition of these Steller sea lion prey from the present study to other collections in the North Pacific Ocean. The following sources were used for comparison: 1. Anthony et al. 2000; 2. Anthony & Roby 1997; 3. Bando 2002; 4. Foy and Paul 1999; 5. Harris et al. 1986; 6. Iverson et al. 2002; 7. Paul and Paul 1998; 8. Paul et al. 1998a; 9. Paul et al. 1998b; 10. Payne et al. 1999; 11. Perez 1994; 12. Sidwell 1981; 13. Stansby 1976; 14. Van Pelt et al. 1997; 15. Worthy & Miculka 1997. Mean energy content ($kJ \cdot g^{-1}$) and proximate composition (± one standard deviation) are given. Where standard deviations were unavailable, ranges were presented. Abbreviations: Bering Sea (BS), British Columbia (BC), Columbia River (Col R), Gulf of Alaska (GOA), northeast Pacific Ocean (NE PO), Prince William Sound (PWS), southeastern Alaska (SEAK), Mature (Mat), Summer (Summ), Continued (ctd.).

Species	$kJ \cdot g^{-1}$	%Lipid	%Protein	%Moist	%Ash	Lth (mm)	Age	Month	Year	Loc	Misc	Source
Eulachon	5.21	4.6-9.0	13.2-15.3	76.5-81.3						Col R		13
	7.49±1.11	14.50	11.08	71.0±3.5		≥100		May-Aug	1995, 1996	GOA		1
	8.42±1.62 (3.3-13.1)	**16.30±4.10 (1.7-28.9)**	**12.35±1.26 (9.7-16.3)**	**69.81±4.46 (61.1-82.5)**	**1.55±0.22 (0.9-3.1)**	**97-224**		**Year-Round**	**2001, 2002**	**SEAK**		**This Study**
	9.08	18.41±1.09	11.79±0.52	68.68±1.53	1.46±0.37	>100		Feb-March	1993	GOA		10
		19.0±2.3				Mean 151		Spring	1994-1998	PWS		6
	9.54	19.45±1.14	12.21±0.48	67.16±1.50	1.69±0.30	>100		June-Sept	1993	GOA		10
	9.9	20.14	12.73			>100		June-Sept	1993	BS		10
	11.1±0.5			64.2±1.7				March & Aug	1984	BS & GOA		11
Herring	3.43	1.43	12.1	84.82	2.06	55		Aug	1993	GOA		10
	3.69±0.56	2.35	17.05	77.6±1.6		<100		May-Aug	1995, 1996	GOA		1
	3.8±0.2					89±0.2	0	March	1996	PWS		7

Table 2.2 ctd.

Species	kJ·g^{-1}	%Lipid	%Protein	%Moist	%Ash	Lth (mm)	Age	Month	Year	Loc	Misc	Source
Herring ctd.		4.7±2.0				Mean 214	≥2	Spring	1994-1998	PWS		6
	4.0±2.9	2.2	18.1	77.6			0	Spring	1995	PWS		2
	4.2					Mean 80	0	Feb	1997	PWS		4
	4.4					Mean 65	0	Oct	1996	PWS		4
	4.9					Mean 77	0	Nov-Dec	1996	PWS		4
	5.7±0.6						≤1	Fall & Spring	1995, 1996	PWS		8
	5.84±1.66	7.42	16.48	72.3±4.5		≥100		May-Aug	1995, 1996	GOA		1
		8.0±3.9				Mean 209	≥2	Summ	1994-1998	PWS		6
	7.1±1.4	9.4	20.3	67.7			1	Spring	1995	PWS		2
	7.44±2.24 (3.0-12.7)	**11.77±6.09 (1.3-25.9)**	**15.69±1.44 (11.0-21.4)**	**69.90±5.94 (58.2-84.1)**	**2.51±0.42 (1.5-3.7)**	**75-280**		**Year-Round**	**2001, 2002**	**SEAK**		**This Study**
	7.96	2.2-23.7	14.2-19.5	59.8-80.3	1.6-2.8					BC - GOA		13
	8.0±1.2						1	Fall & Spring	1995, 1996	PWS		8
	8.58±3.48			68.3±7.9				July-Aug	1984	BS & GOA		11
	10.47			64.7		196		Dec	1999	SEAK		3
	8.8-10.2	13.2-16.6	14.9-15.4	65.4-68.9	2.3-2.5	~155-213		Oct-Nov	1995	PWS		15

Table 2.2 ctd.

Species	kJ·g^{-1}	%Lipid	%Protein	%Moist	%Ash	Lth (mm)	Age	Month	Year	Loc	Misc	Source
Herring ctd.	9.4-10.2						≥2	Fall & Spring	1995, 1996	PWS		8
		14.2±2.7				Mean 217	≥2	Fall	1994-1998	PWS		6
Capelin		1.4±1.0				Mean 131		Summ	1994-1998	PWS		6
	3.54±0.41	2.69±0.98	13.69±0.30	81.32±1.20	2.04±0.13	Mean 114		July-Aug	1993, 1994	GOA	♂	14
	3.8±.0.6	2.7	16.1	79.2			Mat	Spring	1995	PWS		2
		3.2±1.4				Mean 124		Spring	1994-1998	PWS		6
	4.17±1.19	4.05	16.21	77.1±2.83		<90		May-Aug	1995, 1996	GOA		1
	4.51±1.04 (2.7-7.8)	**4.67±2.61 (0.9-13.1)**	**13.97±0.98 (11.3-16.9)**	**78.96±3.27 (69.4-85.8)**	**2.21±0.31 (1.5-3.5)**	**70-140**		**Year-Round**	**2001, 2002**	**SEAK**		**This Study**
	4.67±0.31	4.79±0.67	15.28±0.46	77.81±1.01	1.78±0.11	Mean 105		July-Aug	1993, 1994	GOA	♂	14
	4.96	5.13±1.43	15.38±0.03	78.0±1.0	2.35±0.35	~80-125		Feb	1993	GOA		10
	6.07	8.36±3.24	15.07±0.24	75.09±3.05	2.08±0.08	~80-125		June-July	1993	GOA		10
	6.31	9.57±3.45	14.03±0.44	75.03±2.99	2.02±0.10	~80-125		June-July	1993	BS		10
	7.03±1.21			72.5±2.7				July-Aug	1984	BS & GOA		11
Pollock	2.73±0.26	1.44±0.54	11.84±0.49	83.74±0.60	1.84±0.49	Mean 75		July-Aug	1993, 1994	GOA		14
	3.24±0.31	1.39	16.33	79.2±1.6		≥100		May-Aug	1995, 1996	GOA		1

Table 2.2 ctd.

Species	kJ·g^{-1}	%Lipid	%Protein	%Moist	%Ash	Lth (mm)	Age	Month	Year	Loc	Misc	Source
Pollock ctd.	3.47±0.25	1.48	16.47	79.1±1.2		<100		May-Aug	1995, 1996	GOA		1
	3.5±0.3	1.6	16.7	79.3			0	Spring	1995	PWS		2
	3.6±0.3	1.3	17.6	78.2			2+	Spring	1995	PWS		2
	3.6±0.2					60-110	≤1	Oct	1996	PWS		9
		1.5±0.6				Mean 177	1	Summ	1994-1998	PWS		6
	3.94±0.00	1.58±0.04	14.02±0.52	82.55±0.54	2.58±0.33	~70-80		Aug	1992, 1993	GOA		10
	4.0±0.5					80-110	≤1	March	1996	PWS		9
	4.14±0.73 (2.8-7.0)	**3.19±1.82 (0.1-11.1)**	**14.83±1.25 (10.8-19.6)**	**78.97±2.18 (72.4-83.4)**	**2.98±0.71 (1.6-5.8)**	**70-668**		**Year-Round**	**2001, 2002**	**SEAK**		**This Study**
	4.16	0.6-1.3	16.4-19.3	70.3-82.8	1.1-2.7					BS & NE PO		13
	4.65±0.63			77.5±1.4		430-530		March, July,	1984	BS & GOA		11
		2.3±1.0				Mean 189	1	Fall	1994-1998	PWS		6
	4.2-5.4	1.8-4.5	13.5-16.6	76.9-81.2	3.0-3.7	~148-213		Oct-Nov	1995	PWS		15
		5.10±1.86				Mean 135	1	Spring	1994-1998	PWS		6
	5.46	7.03	13.36	76.56±3.54	2.57	93-322			1982	GOA		5
Hake	4.23	1.4-6.0	12.3-16.0	72.9-82.7	2.8-3.4							12

Table 2.2 ctd.

Species	kJ·g^{-1}	%Lipid	%Protein	%Moist	%Ash	Lth (mm)	Age	Month	Year	Loc	Misc	Source
Hake ctd.	4.96±0.94 (3.0-7.6)	6.17±2.68 (0.4-13.5)	13.51±0.97 (11.3-17.7)	78.14±2.39 (72.4-83.7)	2.32±0.44 (1.5-4.8)	200-660		Year-Round	2001, 2002	SEAK		This Study

Table 2.3. Seasonal proximate composition and whole-body energy content on a wet mass basis by month. Values presented are means (± one standard deviation). For each month, statistically similar species are designated by similar letters. Similarity was determined by ANOVA using Tukey's pairwise tests corrected for multiple comparisons ($p<0.05$).

Energy Content ($kJ \cdot g^{-1}$)	**May-01**	**Sep-01**	**Dec-01**	**Mar-02**	**April-02**	**May-02**	**July-02**	**Sep-02**	**Dec-02**	**Mar-03**
Eulachon	9.35±0.96 a	10.12±1.87 a	8.50±1.55 a	8.41±0.83 a	6.44±0.98 a	8.95±1.45 a	n/a	9.42±0.70 a	9.52±0.71 a	9.14±0.75 a
Herring	6.24±1.28 b	8.04±1.78 b	8.64±1.69 a	5.56±1.16 b	n/a	5.62±1.25 b	4.95±0.87 a	10.59±0.93 b	9.04±1.02 a	5.95±0.94 b
Capelin	n/a	n/a	4.84±0.61 b	4.42±0.70 c	3.28±0.39 b	4.86±0.45 bc	n/a	7.49±0.28 c	n/a	4.48±0.0.68 cd
Hake	3.83±0.62 c	4.61±0.31 c	4.97±0.39 b	5.18±0.65 b	n/a	4.47±0.74 cd		5.29±0.88 d	5.31±0.93 b	4.89±1.40 c
Mature Pollock	3.47±0.44 c	4.84±0.96 c	4.25±0.79 b	4.14±0.57 cd	n/a	3.58±0.46 d	3.30±0.24 b	4.49±0.72 e	4.85±0.67 bc	3.98±0.41 cd
Juvenile Pollock	3.73±0.32 c	4.29±0.55 c	4.60±0.64 b	3.53±0.29 d	n/a	3.75±0.35 d	n/a	4.34±0.67 ef	4.30±0.53 cd	3.62±0.34 d
YOY Pollock	n/a	3.76±0.22 c	4.27±0.51 b	3.42±0.26 d	n/a	3.75±0.33 d	n/a	3.59±0.26 f	4.02±0.35 d	n/a

Table 2.3 ctd.

% Lipid	May-01	Sep-01	Dec-01	Mar-02	April-02	May-02	July-02	Sep-02	Dec-02	Mar-03
Eulachon	18.93±2.80 a	20.60±5.10 a	15.61±4.19 a	16.21±1.90 a	11.59±2.69 a	17.40±3.93 a	n/a	18.54±1.60 a	19.10±1.62 a	18.40±1.85 a
Herring	7.04±3.67 b	13.33±5.23 b	15.18±4.75 a	6.75±2.80 b	n/a	7.10±3.26 b	5.74±2.04 a	20.51±2.57 b	15.87±2.90 b	7.09±2.54 b
Capelin	n/a	n/a	4.98±1.68 b	4.23±1.69 c	1.72±0.54 b	5.86±1.02 b	n/a	12.39±0.73 c	n/a	4.57±1.84 cd
Hake	1.70±1.57 c	5.29±0.88 c	6.28±1.03 b	7.03±1.86 b	n/a	4.79±1.99 bc	n/a	7.00±2.43 d	7.06±2.49 c	6.36±3.68 bc
Mature Pollock	0.73±1.16 c	4.56±2.62 c	3.71±1.97 b	3.31±1.45 cd	n/a	2.16±1.14 cd	1.38±0.49 b	3.96±1.80 e	4.92±1.93 d	3.32±0.96 d
Juvenile Pollock	1.08±0.63 c	2.92±1.32 c	4.36±1.65 b	2.09±0.63 d	n/a	2.28±1.00 d	n/a	3.62±1.69 e	3.68±1.38 d	2.58±1.09 d
YOY Pollock	n/a	2.25±0.89 c	3.91±0.89 b	1.93±0.55 d	n/a	2.42±0.82 cd	n/a	1.84±0.48 e	3.07±0.95 d	n/a

% Protein	May-01	Sep-01	Dec-01	Mar-02	April-02	May-02	July-02	Sep-02	Dec-02	Mar-03
Eulachon	12.22±1.77 a	13.03±0.37 a	13.98±0.80 ab	12.44±1.23 a	11.04±0.74 a	13.00±0.86 a	n/a	13.26±0.91 a	12.72±0.68 a	12.14±0.63 a
Herring	18.30±2.17 b	15.84±1.84 b	15.48±0.45 c	15.45±1.21 b		15.09±1.25 b	14.21±1.82 a	15.53±0.99 b	15.21±0.67 b	16.77±0.84 b
Capelin	n/a	n/a	15.04±0.90 ace	14.32±0.82 cd	13.19±1.02 a	13.56±0.79 ac	n/a	14.80±0.33 bc	n/a	14.02±0.52 c
Hake	16.00±1.23 b	13.33±0.38 a	13.36±0.47 bd	13.02±0.70 a	n/a	13.57±0.78 ac	n/a	13.62±0.61 ac	13.64±0.50 c	12.82±0.69 ad
Mature Pollock	15.93±1.83 b	15.83±1.47 b	14.42±0.87 ae	14.58±0.75 c	n/a	14.15±0.69 cd	13.92±0.56 a	15.14±1.02 bd	15.22±0.66 d	13.76±1.08 c
Juvenile Pollock	16.62±1.43 b	16.05±1.43 b	14.95±0.59 ce	13.76±0.67 cd	n/a	14.54±0.45 bd	n/a	15.01±0.70 bd	14.70±0.61 e	13.33±0.92 cd
YOY Pollock	n/a	14.63±1.15 ab	14.15±1.37 ade	13.54±0.56 d	n/a	14.24±0.22 bcd	n/a	14.51±0.88 cd	14.43±0.45 e	n/a

Table 2.3 ctd.

% Moisture	May-01	Sep-01	Dec-01	Mar-02	April-02	May-02	July-02	Sep-02	Dec-02	Mar-03
Eulachon	67.27±2.84 a	64.98±1.28 a	65.40±1.80 a	69.30±1.78 a	75.80±2.61 a	67.96±3.68 a	n/a	66.84±1.64 a	67.14±2.05 a	69.83±2.07 a
Herring	71.84±3.41 b	68.39±4.22 b	66.48±3.81 a	74.44±3.65 b	n/a	74.49±3.65 b	77.14±3.20 a	61.39±2.22 b	65.97±2.56 a	74.25±2.31 b
Capelin	n/a	n/a	77.51±1.53 b	78.30±2.21 cd	83.11±1.67 b	78.46±1.37 c	n/a	69.89±0.45 a	n/a	79.40±1.91 c
Hake	79.54±1.73 c	79.06±1.13 cd	78.62±1.20 b	77.77±1.75 c	n/a	78.45±2.13 c	n/a	77.43±2.32 c	77.11±2.51 b	79.15±3.47 c
Mature Pollock	79.63±1.50 c	76.56±2.53 c	78.20±2.16 b	78.23±1.67 d	n/a	80.25±1.22 c	81.51±1.12 b	77.75±2.00 c	76.63±1.61 b	81.02±1.28 cd
Juvenile Pollock	79.34±1.50 c	78.31±1.68 d	78.19±1.50 b	80.82±1.00 e	n/a	80.12±0.78 c	n/a	78.90±1.62 cd	78.96±1.31 c	82.29±0.67 d
YOY Pollock	n/a	79.82±1.21 d	78.78±1.82 b	80.94±1.03 e	n/a	80.67±0.86 c	n/a	80.17±0.73 d	80.02±0.94 c	n/a

% Ash	May-01	Sep-01	Dec-01	Mar-02	April-02	May-02	July-02	Sep-02	Dec-02	Mar-03
Eulachon	1.58±0.14 a	1.49±0.12 a	1.66±0.24 a	1.56±0.15 a	1.41±0.12 a	1.71±0.22 a	n/a	1.69±0.37 a	1.48±0.18 a	1.57±0.08 a
Herring	2.82±0.32 bc	2.35±0.29 b	2.22±0.47 b	2.68±0.42 bc	n/a	2.42±0.18 b	2.54±0.30 a	2.37±0.48 b	2.70±0.50 bc	2.70±0.32 b
Capelin	n/a	n/a	2.46±0.16 bc	2.28±0.42 bde	2.28±0.24 b	1.98±0.24 a	n/a	1.99±0.37 ab	n/a	2.28±0.12 c
Hake	2.76±0.51 b	2.42±0.41 bc	2.06±0.20 ab	2.08±0.35 d	n/a	2.59±0.78 b	n/a	2.35±0.30 b	2.44±0.27 b	2.13±0.33 c
Mature Pollock	3.71±1.00 c	3.13±0.69 d	3.22±0.60 d	3.03±0.55 c	n/a	3.49±0.76 c	3.36±0.64 b	3.39±1.05 c	3.22±0.55 d	2.37±0.35 c
Juvenile Pollock	2.96±0.39 b	2.87±0.85 cd	2.73±0.59 c	2.95±0.68 c	n/a	2.79±0.33 b	n/a	2.94±0.78 bc	2.70±0.60 bc	2.07±0.23 c
YOY Pollock	n/a	2.68±0.25 bcd	2.75±0.26 cd	2.76±0.29 ce	n/a	2.62±0.21 b	n/a	2.74±0.29 bc	3.06±0.67 cd	n/a

Table 2.4. Seasonal proximate composition and whole-body energy content on a wet mass basis pooled over the two sampling years. Values presented are means (± one standard deviation). Asterisks indicate months for which values were statistically different between years. For each month, statistically similar species are designated by similar letters. Similarity was determined by ANOVA using Tukey's pairwise tests corrected for multiple comparisons ($p<0.05$).

Energy Content ($kJ \cdot g^{-1}$)	May	July	Sept	December	March	April
Eulachon	9.08±1.31 a	n/a	9.64±1.20 a*	9.13±1.19 a	8.77±0.86 a	6.44±0.98 a
Herring	5.73±1.25 b	4.95±0.87 a	9.32±1.90 b	8.89±1.31 a	5.74±1.07 b	n/a
Capelin	4.86±0.45 c	n/a	7.49±0.28 c	4.84±0.61 bc	4.45±0.68 c	3.28±0.39 b
Hake	4.22±0.75 cd	n/a	5.06±0.81 d	5.22±0.82 b	5.04±1.06 d	n/a
Mature Pollock	3.54±0.45 d	3.30±0.24 b	4.72±0.89 de	4.61±0.77 bc	4.08±0.52 ce	n/a
Juvenile Pollock	3.75±0.34 d	n/a	4.31±0.59 ef	4.43±0.59 c	3.56±0.31 e	n/a
YOY Pollock	3.75±0.33 d	n/a	3.67±0.25 f	4.12±0.43 c	3.42±0.26 e	n/a

Table 2.4 ctd.

% Lipid	May	July	September	December	March	April
Eulachon	17.88±3.64 a	n/a	19.18±3.18 a*	17.78±3.29 a	17.31±2.16 a	11.59±2.69 a
Herring	7.09±3.26 b	5.74±2.04 a	16.92±5.45 b	15.61±3.69 b	6.90±2.65 b	n/a
Capelin	5.86±1.02 b	n/a	12.39±0.73 b	4.98±1.68 cd	4.37±1.73 c	1.72±0.54 b
Hake	3.56±2.37 c	n/a	6.43±2.18 c	6.84±2.19 c	6.71±2.85 b	n/a
Mature Pollock	1.60±1.33 c*	1.38±0.49 b	4.35±2.37 d	4.43±2.02 d	3.31±1.27 cd	n/a
Juvenile Pollock	2.03±1.05 c	n/a	3.15±1.47 de	4.00±1.53 d	2.26±0.84 d	n/a
YOY Pollock	2.42±0.85 c	n/a	2.05±0.73 e	3.41±1.00 d	1.93±0.55 d	n/a

% Protein	May	July	September	December	March	April
Eulachon	12.76±1.24 a*	n/a	13.19±0.78 a	13.19±0.95 a*	12.29±0.98 a*	11.04±0.74 a
Herring	15.66±1.88 b	14.21±1.82 a	15.68±1.47 bc	15.93±0.69 B	16.05±1.24 b	n/a
Capelin	13.56±0.79 ac	n/a	14.80±0.33 ab	15.04±0.90 cd	14.20±0.72 cd	13.19±1.02 b
Hake	14.54±1.55 bc*	n/a	13.52±0.56 a	13.56±0.50 a	12.93±0.69 e	n/a
Mature Pollock	14.84±1.52 b*	13.92±0.56 a	15.59±1.37 b	14.89±0.84 c	14.28±0.96 c	n/a
Juvenile Pollock	14.97±1.12 b*	n/a	15.71±1.32 b*	14.82±0.61 cd	13.61±0.78 df	n/a
YOY Pollock	14.24±0.22 abc	n/a	14.57±1.00 c	14.32±0.92 d	13.54±0.56 cdef	n/a

Table 2.4 ctd.

% Moisture	May	July	September	December	March	April
Eulachon	67.75±3.41 a	n/a	66.26±1.75 ab*	66.48±2.11 a	69.56±1.92 a	75.80±2.61 a
Herring	74.02±3.70 b	77.14±3.20 a	64.89±4.86 a	66.16±3.07 a	74.35±3.07 b	n/a
Capelin	78.46±1.37 c	n/a	69.89±0.45 b	77.51±1.53 bc	78.75±2.14 cd	83.11±1.67 b
Hake	78.89±2.01 c	n/a	77.97±2.13 cd	77.54±2.30 b	78.42±2.76 d	n/a
Mature Pollock	80.01±1.35 c	81.51±1.12 b	76.94±2.41 c	77.26±1.99 b	79.27±2.04 cd*	n/a
Juvenile Pollock	79.96±0.99 c	n/a	78.50±1.67 d	78.60±1.44 bc	81.34±1.14 e	n/a
YOY Pollock	80.67±0.86 c	n/a	79.99±0.99 d	79.53±1.46 c	80.94±1.03 ce	n/a

% Ash	May	July	September	December	March	April
Eulachon	1.67±0.21 a	n/a	1.63±0.33 a	1.55±0.22 a*	1.56±0.12 a	1.41±0.12 a
Herring	2.49±0.26 b	2.54±0.30 a	2.36±0.39 b	2.52±0.54 bc	2.69±0.37 b	n/a
Capelin	1.98±0.24 a	n/a	1.99±0.37 abc	2.46±0.16 bcd	2.28±0.32 c	2.28±0.24 b
Hake	2.66±0.67 b	n/a	2.37±0.34 b	2.33±0.30 b	2.10±0.34 c	n/a
Mature Pollock	3.57±0.85 c	3.36±0.64 b	3.22±0.83 d	3.22±0.56 e	2.79±0.58 B	n/a
Juvenile Pollock	2.83±0.34 b	n/a	2.89±0.82 cd	2.72±0.58 cd	2.64±0.70 b*	n/a
YOY Pollock	2.62±0.21 b	n/a	2.71±0.27 bc	2.94±0.56 de	2.76±0.29 b	n/a

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GENERAL CONCLUSION

One hypothesis for the large declines in piscivorous predator populations since the 1970's in the North Pacific Ocean and Bering Sea is the nutritional stress hypothesis which describes a lack of quality prey. The two premises the hypothesis is founded upon are (1) prey quality of a single prey species is consistent among individuals and over time, and (2) forage fish are consistently superior quality prey items to groundfish. In this systematic study addressing prey of Steller sea lions which are one of the declining species, I found these premises to be incorrect. Prey quality varies significantly by season in a cyclical manner related to the life history of the fish, particularly for the forage fish. These seasonal cycles are slightly asynchronous among fish species, causing overlap such that no one species is consistently a better prey item. Though in general eulachon and herring tended to be better prey items than pollock and hake, there were times of the year when forage fish typically characterized as "high-energy" and "high-fat" prey were similar in body composition to groundfish thought of as "low-energy" and "low-fat". Furthermore, I found that though the prey quality of capelin was highly dynamic similar to the other forage fish species, the energy and lipid content was lower and more similar to the groundfish species. In conclusion, it is critical that season be accounted for when considering foraging-related bioenergetics of Steller sea lions and other pinnipeds.

APPENDIX 2.1:

Rationale for selection of energy coefficients to calculate energy content from proximate composition.

Values of energetic equivalents vary in the literature based on the discrepancy between gross heats of oxidation and net metabolizable energy which accounts for incomplete oxidation of nutrients in the body, a difference particularly pertinent to nitrogenous compounds (Watt and Merrill 1963). Net metabolizable energy is very difficult to estimate, however, as it is species-specific, and has only been estimated for several herbivorous animals. Additionally, metabolizable energy depends on the animal's nutritional state, making the quantification of incomplete oxidation extremely difficult. As such, a common practice has been to reduce energetic equivalents by somewhat arbitrary amounts to roughly estimate net metabolizable energy (Robbins 1993; Brody 1945).

Reported energy equivalents range from 34.75 – 40.15 $kJ \cdot g^{-1}$ for lipid and 16.75 – 23.86 $kJ \cdot g^{-1}$ for protein, while that of carbohydrates varies less, ranging from 15.57 – 18.33 $kJ \cdot g^{-1}$ (Anthony et al. 2000; Payne et al. 1999; Robards et al. 1999; Van Pelt et al. 1997; Brett 1995; Montevecchi and Piatt 1984; Sidwell 1981; Watt and Merrill 1963; Brody 1945). The variability in lipid equivalents relates to the degree of saturation of the constituent fatty acids. Saturated fats have greater energy densities than unsaturated fats, a phenomenon which may be significant in different species of fish or those that utilize the alternate classes of fatty acids during different life history stages (Brett 1995; Robbins 1993). Though many energetic studies concerning North Pacific Ocean species use the

energy equivalent of 39.57 $kJ \cdot g^{-1}$, this is a mean value of 'meat' calculated from a compilation of oxidation studies (Brody 1945). This value is likely an overestimate for fish which tend to have relatively large quantities of unsaturated fat (Iverson et al. 2002; Morris and Culkin 1989), and thus the equivalent suggested by Brett of 36.43 $kJ \cdot g^{-1}$ which is a mean value for fish was used in this study (1995).

The variation in protein equivalents is primarily a relic of alternative methods of estimating net metabolizable energy (Watt and Merrill 1963). The largest discrepancies occur between predators with different metabolic pathways, with uricotelic animals such as birds having smaller energetic equivalents than other consumers due to their relatively lesser efficiency in nitrogen use. Estimates of the usable portion of ingested nitrogen varies with other factors as well, including amino acid composition, consumer age, and reproductive state, making estimation of metabolizable energy an extremely difficult task (Watt and Merrill 1963; Brody 1945). The energetic equivalent of 23.66 $kJ \cdot g^{-1}$, a value also derived from an unknown 'meat' source, has been employed in several North Pacific energetics studies (Anthony et al. 2000; Van Pelt et al. 1997). The equivalent of 20.10 $kJ \cdot g^{-1}$ has been suggested to be more appropriate for fish and was therefore used in this study (Brett 1995).

Energetic equivalents for carbohydrates remain relatively constant in the literature because they can be fully oxidized physiologically (Anthony et al. 2000; Van Pelt et al. 1997; Brett 1995). Thus, the combustion value of 17.17 $kJ \cdot g^{-1}$ was used.

The high correlation between bomb calorimeter measurements of energy content and energy content calculated using energy equivalents demonstrated an appropriate selection of equivalents used.

APPENDIX 2.2

Rationale for selection of protein determination method.

Among the many methods to determine protein content, several of the more-commonly used techniques measure protein content in an indirect manner, in which nitrogen content is measured to which correction factors are applied to estimate protein content. The reason for the indirect approach is that these methods are more expedient and cost effective than direct measurements, despite known limitations of the methods. One method used in several North Pacific fish composition studies is the determination of ash-free dry lean matter (AFDLM), 94% of which is assumed to be protein. For this method, samples are dried and lipid is extracted. The remaining pellet is incinerated to obtain ash content while the portion incinerated, the AFDLM, is multiplied by 0.94 (Anthony et al. 2000, Robards et al. 1999; Van Pelt et al. 1997). Another method used is the separate analysis of different proximate fractions followed by calculation of protein content by difference; that is, 100% - lipid content (%) – moisture content (%) – ash content (%). This method includes the small amount of carbohydrates which are assumed to be negligible in the estimated protein fraction (Worthy and Miculka 1997).

Another commonly-used method to measure protein content indirectly employed in this study is the measurement of total nitrogen content and multiplication of this value by a conversion factor to account for the nitrogen content of protein (Leco Instruction Manual 2001; Craig et al. 1978). Development of this method dates back to the early 1900's (Jones 1931), however it remains a common practice today (Bando 2002; Lourenco 2002). The conversion factor of 6.25 was originally determined from the

findings that animal-derived protein (primarily blood serum and milk) contains 16% nitrogen:

$$\text{Nitrogen - To - Protein Conversion Factor} = \frac{100}{\text{Nitrogen Content of Protein}}$$

The limiting factor of this technique is the accuracy of the conversion factor. Proteins are composed of a suite of amino acids containing different amounts of nitrogen, ranging from 14-20% nitrogen for plant- and animal-derived proteins (conversion factors range from 5.0 - 7.14). The few analyses limited to animal muscle proteins including chicken, halibut, scallop and shrimp, range from 16.1 – 17.0 (conversion factors range from 5.9 - 6.2), with halibut fillets containing 16.5% nitrogen (conversion factor = 6.06) (Jones 1931). The most pertinent conversion factor of 6.06 was selected for use in this study. This value pertains to muscle protein only, however, and is probably not valid for whole fish. Nonetheless, the accuracy of the conversion factor does not appear to be a problem due to the high correlation between bomb calorimeter measurements of energy content and energy content calculated using estimated protein content